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A STUDY OF NEOTROPICAL DIDELPHIS (MAMMALIA, POLYPROTODONTIA, DIDELPHIDAE)

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ABSTRACT

The Haffer-Vanzolini model proposes that geographical variation and speciation of terrestrial organisms in South America can be explained in terms of the influence of pleistocenic climatic changes on vegetational distribution. During dry periods forests were restricted to small areas, which acted as "refuges" for sylvatic organisms. Geographical differentiation and sometimes speciation were a consequence of this isolation.

In a preliminary survey of numerous mammalian taxa, it was found that distribution patterns concorded well with the model, which also suggested explanations for the origin and extinction of species and higher taxa. The ecology of any taxon must however be taken into account when considering how paleolandscapes might have influenced its present distribution.

The genus Didelphis was studied in detail. The major climatic, orographic and vegetational factors relating to 289 locality records were analysed. It is shown that one ensemble of the D. albiventris group inhabits dry deciduous forests, meadows, Thornbush (Caatinga and Chaco), the Monte and the Cerrados. Another ensemble is associated with the Oreal domains of the Andes, but avoids higher altitudes with extremes of dry and cold. These two ensembles appear to be linked through the Monte domain. The D. marsupialis group is restricted to rainforests and cloud forests. Those inhabiting northern South America are separated by at least 800 kilometers from an ensemble of populations living in the Atlantic and Araucaria forests.

Goegraphical variation of the D. marsupialis group along transects linking sampling localities was assessed statistically and it is shown that the patterns of variation are well in agreement with the Haffer-Vanzolini model. Correlation pleiades show differences between the ensemble of populations in northern South America and those in eastern Brazil, and it is suggested that these two ensembles are distinct at the species level.

The observed differences in correlation pleiades between females and males is discussed. Some data on reproduction of D. Albiventris is presented.

TO

Mario Aragão

who teached me to have biological imagination

Graziela Barroso

who showed me the wonders of the rainforest

Zezé and Ana

who gave me love

to my people

I think I could turn and live with animals, they are so placid
and self-contain'd
I stand and look at them long and long
They do not sweat and whine about their condition
They do not lie awake in the dark and weep for their sins,
They do not make me sick discussing their duty to God,
Not one is dissatisfied, not one is demented with the mania
of owning things,
No one kneels to another, nor to his kind that lived thousands
of years ago,
Not one is respectable or unhappy over the whole earth.
So they show their relations to me and I accept them...

Walt Whitman, Song of Myself

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CHAPTER I

INTRODUCTION

1.1 INTRODUCTION

Opossums of the genus Didelphis are the largest extant New World marsupials. They are common animals exploiting a wide range of habitats from Southern Canada to Central Argentina.

Hershkovitz (1949a, 1951) in a discussion of the nomenclature of the genus pointed out that Didelphis Linnaeus, 1758 was in fact a composite name but that the subsequent usage restricted it to the common opossums. Cabrera (1957) in his catalogue recognized two species each one with two subspecies in South America. Hall and Kelson (1959) included all Middle and North American forms in a single species, Didelphis marsupialis Linnaeus, 1758. Gardner (1973) as a result of morphometric and cytogenetic studies recognized that the North American Opossum (D. virginiana, Kerr, 1792) was specifically distinct from D. marsupialis from Central and South America. Hershkovitz (1969, 1972) noted that Didelphis azarae Temminck, 1825, the name then commonly used for the White Eared Opossum in South America, was based on specimens of more than one species. The next available name for that species is Didelphis albiventris Lund, 1841.

Recent reviewers of Marsupial Biology (Hershkovitz, 1972; Hunsacker, 1977; Reig et al., 1977; Reig et ál., in preparation) have recognized three species: D. virginiana the North American Opossum; D. marsupialis, the Neotropical Black-Eared Opossum and D. albiventris, the White-Eared Opossum.

The taxonomic arrangement of the genus in South America can be summarized as follows:

Didelphis marsupialis Linnaeus, 1758

Didelphis marsupialis marsupialis Linnaeus, 1758

Didelphis marsupialis aurita Wied, 1826

Didelphis albiventris Lund, 1841

Didelphis albiventris albiventris Lund, 1841

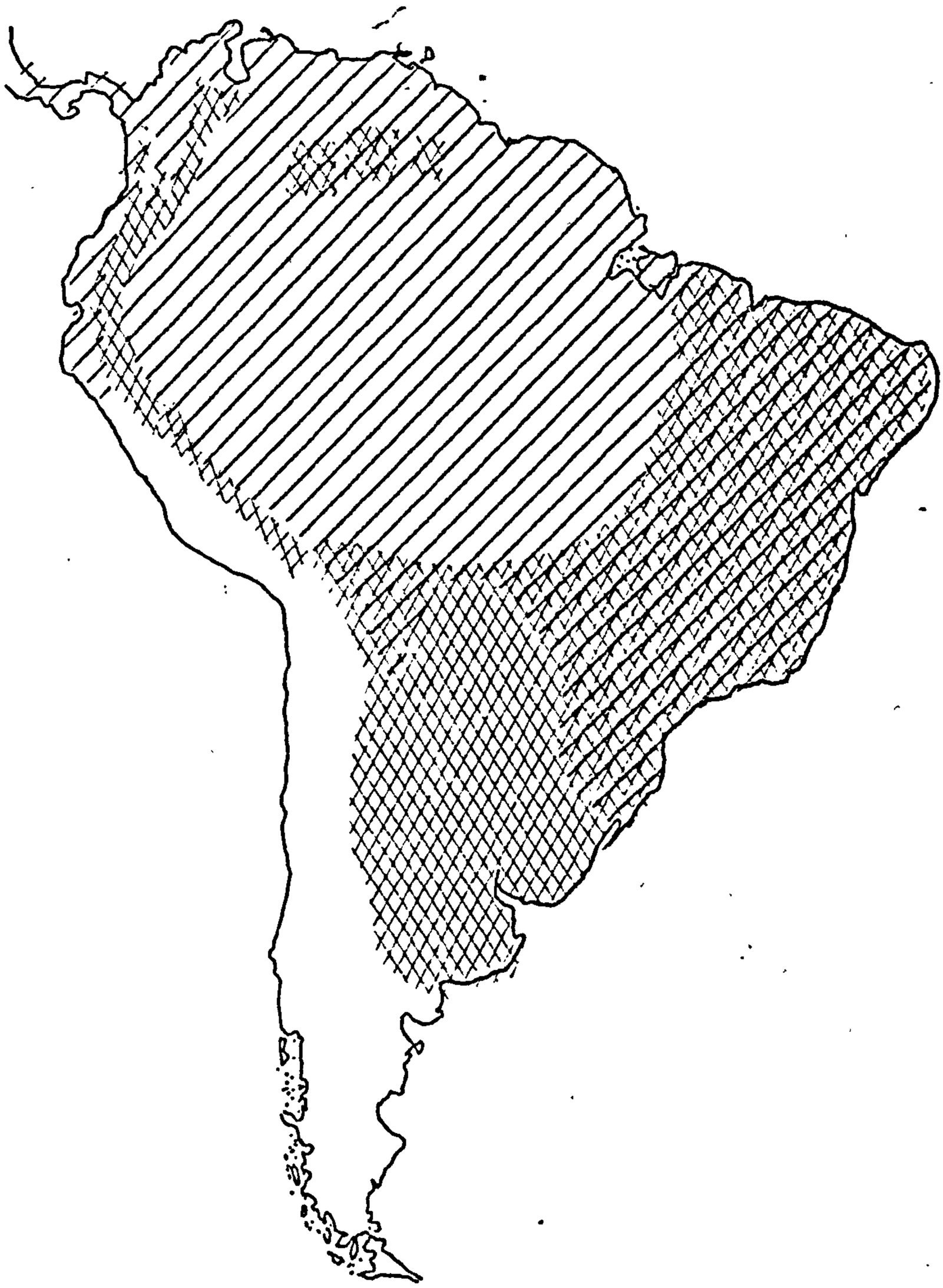
Didelphis albiventris azarae Tschudi, 1844

This arrangement is based on Cabrera (1957) modified to take into account the recent changes in nomenclature discussed above.

The most recent review of the distribution on Didelphis in South America is that of Hershkovitz (1972) (Figure 1.1).

While working in the Museu Nacional, Rio de Janeiro, I noticed that there ppeared to be a discrepancy between the published accounts of the distribution of the different species of Didelphis in South America (Hershkovitz, 1972 and subsequent authors following him, e.g. Tyndale-Biscoe, 1973 and Hunsaker, 1977) and the locality records of specimens in the Museum. According to these authors, D. marsupialis is an animal living at low altitudes and D. albiventris is a temperate zone species. However, even a cursory inspection of the collections at the Museu Nacional, shows that the two groups are usually allopatric, contrary to the impression given by figure 1.1. Moreover, both species are found in localities which have the same altitude and temperature.

After this discovery, I decided to study in detail the distribution of Didelphis in South America. At the same time, I started to study the geographic variation of both D. marsupialis and D. albiventris. I believe that in order to explain a pattern of distribution observed in a species, it is important to have a basic knowledge of both the geographical ecology and the geograph-



Black-eared Opossum

White-eared Opossum

Figure 1.1 - Hershkovitz's(1969,1972) distribution of the Opossums of the Genus Didelphis in South America.

ical variation of the populations concerned. The study of the ecological factors underlying the distribution of a species is not only of interest in itself, but may also give some insight into the processes leading to morphometic variation.

Subsequently, I read the paper of Vanzolini (1970) about Systematic Zoology, Geography and the origin of species. In this paper Vanzolini sets out the Refuge Theory of origin of complex Neotropical biotas, the Haffer- Vanzolini model. I decided to see whether the data collected on the distribution and variation of Didelphis in South America could be explained in terms of this theory.

In the remainder of this chapter, I present the methods used in this study. Chapter two is devoted to the examination of the Haffer-Vanzolini model and to the implications of this model for the studies on the relationship between the South American landscape and the patterns of distribution of mammalian taxa. Chapter three is concerned with the Ecology of Didelphis. Chapter four examines the geographical variation of the Black Eared Opposum in South America. The last chapter is an attempt to explain the present distribution and variation of the Black Eared Opossum in terms of the ideas discussed in the previous chapters.

The chapters in this thesis are arranged in the order in which they were written. The ideas presented in the interim discussions were used to develop arguments which are critically examined in the subsequent chapters.

The study of the variation of the White Eared Opposum is not yet complete and will be object of a future report.

1.2 DATA

1.2.1 Specimens

The number of specimens examined exceeds 1400. It is divided between Black and White Eared Opossums in approximately equal numbers. In addition to these specimens, 662 cards with records of capture of White Eared Opossums in the Northeast of Brazil were also examined. Of that total number, 318 correspond to specimens examined by me. These cards are deposited at the Museu Nacional, Rio de Janeiro.

The abbreviations listed below correspond to the institutions in which the material examined is housed.

BM - British Museum (Natural History), London

FM - Field Museum of Natural History, Chicago

KU - University of Kansas Museum of Natural History, Lawrence

LM - Rijksmuseum van Naturlijke Historie, Leiden

MG - Museu Paraense Emilio Goeldi, Belém

MN - Museu Nacional, Rio de Janeiro

MP - Muséum National d'Histoire Naturelle, Paris

MVZ - Museum of Vertebrate Zoology, University of California, Berkeley

MZ - Museu de Zoologia da Universidade de São Paulo, São Paulo

ZSM - Zoologisches Staatssammlung, Munchen

AP - Coleção A. Perachi, Departamento de Biologia Animal, Universidade Rural, Seropedica

1.2.2 Data on Reproduction

The material used was collected during the course of a research project on Plague endemics. This project was conducted by the former Servico Nacional de Peste (SNP, National Plague Service, Brazilian Ministry of Health). The collecting of specimens was supervised by professor J. Moojen. One card was issued for each specimen caught. In these cards, information about environmental conditions, reproductive state, ectoparasites, testing for plague and some measurements of the animal, were written.

1.2.3 Ecological Data and Localities

At least one specimen was examined from 289 localities. these localities are listed in appendix II ,

for the collecting localities of the Black Eared Opossum. Information concerning these localitics came from a large variety of sources. For each locality, I tried to obtain the geographical coordinates and the altitude. For this information, I used Hershkovitz (1977); American Geographical Society's "Map of Hispanic America" (Peruvian sheets); the IBGE's "Mapa do Brasil ao Milionesimo"; some RADAM maps (BRASIL, Departamento Nacional da Producao Mineral, several dates); The Times' "Atlas of the World"; the "Geografia do Brasil" (BRASIL. Fundacao Instituto Brasileiro de Geografia e Estatistica, 1977); and the several volumes of IBGE's "Enciclopedia dos Municipios Brasileiros."

The following set of climatic normals was tried to be obtained from each locality: Annual mean temperature; annual mean of maxima temperature; annual mean of minima temperature; mean of

annual total rainfall; mean annual nebulosity (in tenths); index of Tornthwhite for effective rainfall (according to the formula given by Setzer, 1946); number of months with more than 100 mm of rainfall; number of months with rainfall between 100 mm and 30 mm; and the number of months with less than 30 mm of rainfall. When a reliable source was found, I used the Koeppen classification as well. A preliminary investigation showed me that these features were the easiest to obtain among the ones being related with the case in study. A complete set of data was obtained for most of the Brazilian localities. Unfortunately, the set is almost always incomplete for the rest of the continent. The climatic data were gotten from the following sources: For Brazil, the "Normais Climatologicas" (of which I could only get the two volumes which are in print, BRASIL. Ministerio da Agricultura, .1970); the "Atlas Climatologico" (BRASIL. Ministerio da Agricultura, 1969); and, for the State of Sao Paulo, Setzer (1946). These sources were complemented by the above-mentioned "Geografia do Brasil." Excepting Brasil and Argentina, there are few localities with meteorological stations. I could get data from South American localities other than Brazil, using, for Ecuador, Acosta y Solis (1965), and Cordovez (1962); for Venezuela, Rohl (1955). Some mean temperatures were obtained using the formula of Eidt (1968). A general classification of the South American climate is found in this latter paper, as well as in Steward (1952). However, this latter work is, on the whole, outdated. Some other normals were obtained from the World Weather Records, published by the Smithsonian Institution (Clayton, 1927, 1934; Clayton and Clayton, 1947).

Other environmental features I used were drawn from a variety of sources: the above-mentioned records of capture deposited

at the Museu Nacional, Rio de Janeiro; Ab'Saber (1971, 1977a); Acosta-Solis (1965); Aparici & Difriri (1953); Aragao (1961); Askew et al. (1971); Azevedo (1968); Barret (1979); BRASIL. Departamento Nacional da Producao Mineral (1973a, 1973b, 1973c, 1974a, 1974b, 1975); BRASIL. Fundacao Instituto Brasileiro de Geografia e Estatistica (1977); Beard (1953); Cabrera (1953); Cabrera & Willink (1973); Chapman (1926); Cordovez (1962); Cuatrecasas (1958); Ducke (1959); Ducke & Black (1953); Drewes & Drewes (1957); Ferri (1963b, 1971); Fittkau et al. (1968); Graham (1973); Haffer (1970); Hershkovitz (1962, 1969, 1972); Hills & Randall (1968); Hueck (1972); Laborieau (1966); Andrade-Lima (1966a,b); Maack (1968); Mares (1975); Meggers (1973); Morello (1958); Muller (1973); Pearson (1951); Richards (1952); Rizzini & Heringer (1962); Steward (1950); Takeuchi (1960a, 1960b, 1960c); Tate (1938, 1939); Toledo (196); Weberbauer (1945) Valverde et al. (1962); Van der Hammen (1974); Vanzolini (1972, 1976); Veloso (1946, 1966); Vila et al. (1965). To the above, I must add that I had some field experience in the Atlantic Forest Domain and some in the Caatinga Domain.

1.2.4 Measurements

The measurements were taken using a dial caliper graduated in twentieths of a millimeter. Only skull measurements were made and used. Each specimen was assigned to one of eight age classes - (numbered from nought to seven) according to system based on tooth eruption and wear. The system was devised by Gardner and modified by Tyndale-Biscoe & Mackenzie (1976). Only individuals belonging to age classes six and seven were measured, except the samples from the Northeast of Brazil which had all specimens measured for some

characteristics. The skull dimensions used are the ones proposed by Gardner (1973) which are of general usage. I did one dimension more, the length of Nasals. The list below gives the dimensions and the abbreviations used throughout this thesis.

GLS - Greatest Length of Skull

CB - Condylobasal Length

PL - Palatal Length

Z - Zygomatic Breadth

IC - Interorbital Constriction

COP - Postorbital Constriction

CAN - Breadth Across Canines

BAM - Breadth Across Molars

BBC - Breadth of Brain Case

BPS - Breadth of Palatal Shelf

MAX - Length of Maxillary Toothrow

SM - Length of Upper Molar Series

MAD - Length of Mandible

SIM - Length of Lower Molar Series

ROS - Breadth of Rostrum Across Jugals

GBN - Greatest ~~Length~~ Breadth of Nasals

RAF - Breadth of Rostrum Across Frontals

NAS - Length of Nasals - The greatest length obtainable of the right nasal.

In this report, 300 odd specimens of the Black Eared Opossum were measured and used to study the geographical variation. The measurements taken were lumped according to localities (see below) and punched in computer cards. All basic computations were then made from these cards. The basic statistics of each sample

used in the study of geographic variation are shown in a series of tables in chapter four.

1.3 METHODS

The basic theoretical assumption in this thesis is that geographical speciation is the basic process of evolution at the species level (MacArthur, 1972; Mayr, 1942, 1963). The model used is the above-mentioned Haffer-Vanzolini model (Vanzolini, 1970, 1973). The basic approach reflects the nature of the samples available. Given the small number of specimens in each sample, and the distance between the sampling localities, I realized that the method used by Vanzolini and Williams (1970) was appropriate. The characters were analyzed along transects. The transects are usually an approximately linear series of localities and at least one major sample is always present in each transect. Before the construction of the transects, the major samples were first studied together. The result of these studies, the hypothesis that core areas should appear in regions where "refuges" existed, and the availability of samples orientated the choice of the transects to be analysed.

The sexes were studied separately, since it is expected that sexual dimorphism could occur. I did not study the dimorphism in each character but the correlation pleiades of character in each sex. This study confirmed that the decision to study the characters separately was correct. Althought the transects are approximately the same for both sexes, since not all the localities had samples for each sex, some localities which appear in the transect of one sex will not do so in the transect of the other.

After studying the variation of each character along the transects and summarizing the differentiation found, the results were compared in order to establish "core areas". The whole method is explained in detail in Vanzolini & Williams (op. cit.)

1.3.1 Samples and Transects

I have called "major samples" those which had a minimum of five individuals; samples with less specimens than that were considered "minor samples". Vanzolini & Williams (op. cit.) considered the construction of the major samples under geographical criteria and gave three orders of stringency: 1. samples from one single and well-defined locality; 2. an ecologically homogeneous group of close-set localities; and 3. a group of not so close, but still ecologically homogeneous localities. To those three orders I may add a fourth, a sample drawn from the literature on which I had, of course, not too much control.

The ideal sample is the first one. But the material available for studies in South American Mammalogy is such that it limits the student to use any sample which can obey those orders of stringency. Only one sample, from a set of localities in Panama belongs to the fourth type. However, the indications given by Gardner (1973) from whom the sample was drawn, assured me that it can be considered as being of the type three. Since I found this sample to be very important to my analysis, I decided to use it. There were no samples which were exactly of the third type, but at worst, were intermediate between the third and the second. Even without having samples of the third type only, the results of the analysis is worthy, but in the particular case of Black

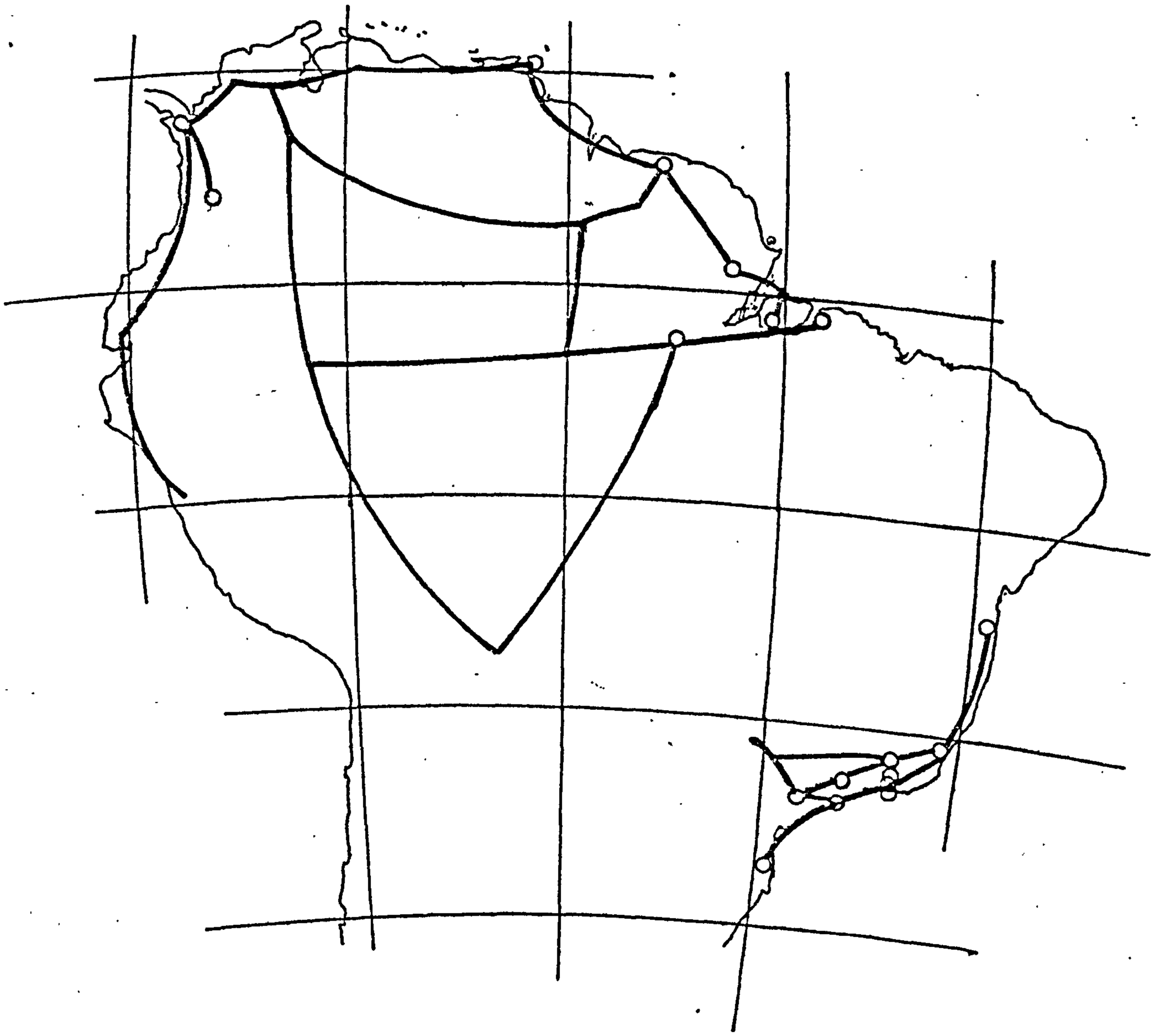


Figure 1.2 - Transects

Circles, major samples

Eared Opossums, they must be seen only as provisional results which can be somewhat modified by further research. On the other hand, Opposums having no territory or definite social structure, and being ubiquous in almost every habitat, do not have well-defined demes, as in the case for instance of the Cricetid Holochilus Cerqueira, 1976). Therefore, the "local population" sampled is actually a sample in a somewhat continuous distribution of individuals. And the shortcomings of the method used are but a few.

When studying the correlations intra and interlocality, I suspected that there was a strong differentiation between the Opossums of the Atlantic Forest and Northern South America. Therefore these two sets were studied separately. Chapterfour shows the evidence and discusses the issue.

A list is given below of the transects, which are pictured in the map figure 1.2. The abbreviations are the same for males and females, each sex being distinguished in the text, tables and figures by the last digit, F for females and M for males.

Transects of Tropical Atlantic and Araucaria Domains (Eastern Brazil)

1. Coastal Transect

Smg - Sao Miguel, Alagoas

IlH - Ilheus, Bahia

ESP - Espirito Santo (Serra, Vila Velha, Morro de Argola, Santa Tereza Campinho)

Sma - Serra de Macae, Macae, Rio de Janeiro

Cas - Casimiro de Abreu, Rio de Janeiro

GBT - Floresta da Tijuca, Rio de Janeiro, Rio de Janeiro

BFL - Baixada Fluminense (Barro Branco, Sarapui (Municipio de Caixas), Iataguai, both Rio de Janeiro)

Mng - Mangaratiba, Rio de Janeiro

Lit - Litoral de Sao Paulo (Boraceia, Bertioga, Caraguatatuba, Ubatuba, all Sao Paulo)

Ban - Serra do Bananal, municipio de Serrinha, Parana

SCA - Santa Catarina (Joinville and Humboldt colony)

2. Ilheus-Bananal Transect

ILH -

ESP -

ZMM - Zona da Mata de Minas Gerais (Juiz de Fora and Alem Paraiba)

Sjm - Sao Joao Marcos, Rio de Janeiro

VAP - Vale do Paraiba, Sao Paulo (Piquete, Cruzeiro and Taubate)

COT - Cotia, Sao Paulo

Ban -

3. Litoral-Lins Transect

LIT -

COT -

Cap - Campinas, Sao Paulo

Pdc - Pocos de Caldas, Minas Gerais

Itu - Ituverava, Sao Paulo

4. Tijuca-Lins Transect

GBT -

BFL -

TER - Terezopolis, Rio de Janeiro

Sjm -

ZMI -

Pdc -

Itu -

Figure 1.3 - Collecting localities studied. Eastern Brazil

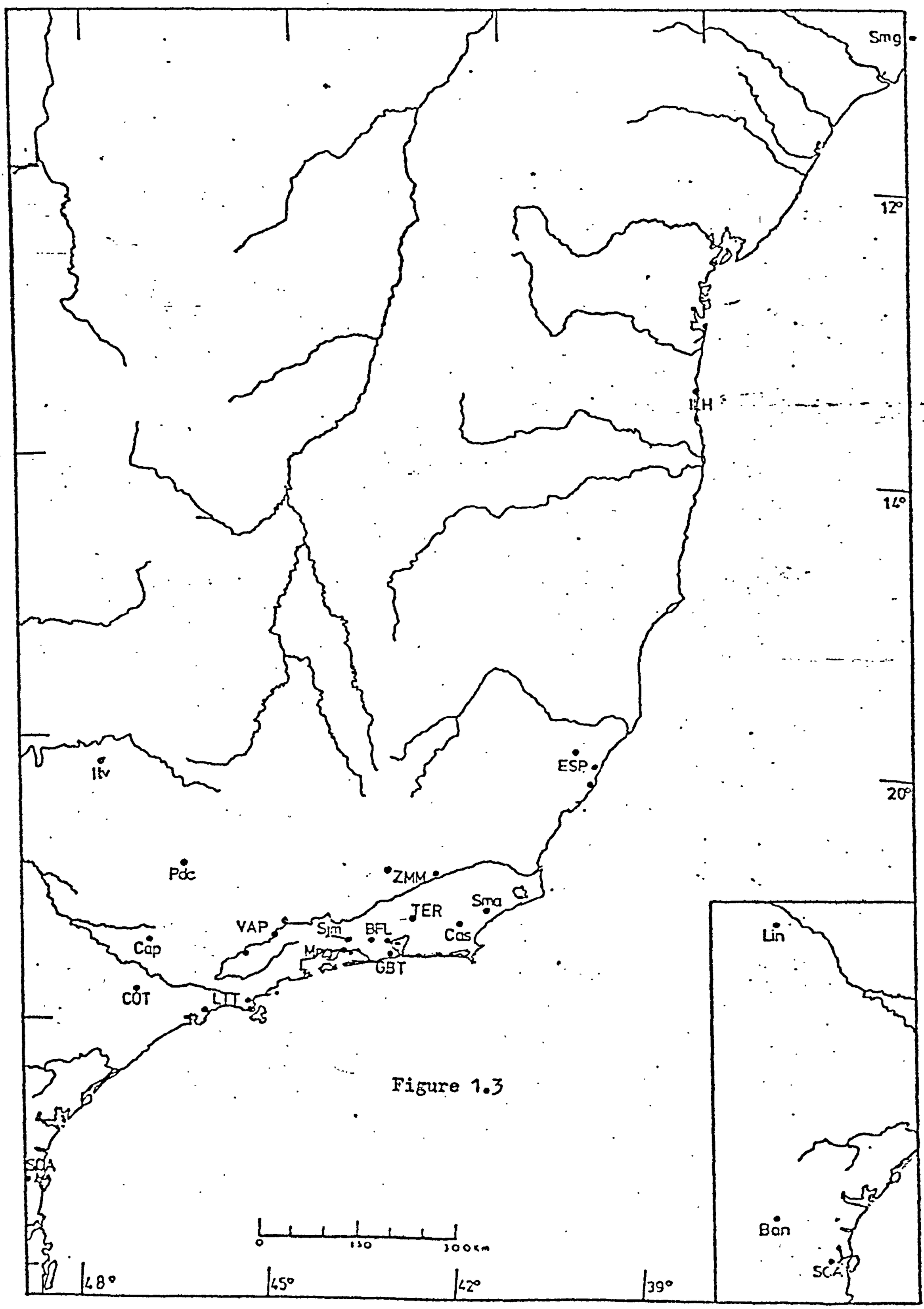

Smg
12°
14°
20°
Itv
ESP
Pdc
ZMM
JER
Sma
VAP
Sjm
BFL
Cas
Cap
Mrg
GBT
COT
LIT
Lin
Ban
SCA
0
150
300km
48°
45°
42°
39°

Figure 1.3

Lin -

5. Santa Catarina-Lins Transect

SCA -

Ban -

Lin -

The transects are not exactly the same for both sexes, females have no samples from Sma, Pdc, Itu, and Lin. LIT is a major sample for females, but ESP is a minor one. The males have all samples except Cas. Samples abbreviated in capital letters are the major ones.

One locality, Sao Francisco Xavier, Serra da Mantiqueira was too imprecise and was not used.

These transects are approximately linear, getting lateral localities in it. However transects three and four are sweeper-like. The three samples farther west, Pocos de Caldas, Ituverava and Lins, are very far from the major samples with which they are compared, the results needing to be taken cautiously.

Transects of Northern South America

1. Belem-San Nicolas Transect

BEL - Belem, Para (Belem, Nova Timbotena, Guama, Utinga, Anandeua)

Cmt - Cameta, Para

CAL - Caldeirao, Para

CUR - Curralinho, Para

STM - Santarem Para (Santarem, Caricatuba and Taperinha)

Pau - Pau de Letra, West Tapajos, Para

Itc - Itacoatiara, Amazonas

Man - Manaus, Amazonas

Sni - San Nicolas, Amazonas, Peru

2. Santarem-Buenavista Transect

STM -

Pau -

Cax - Caxirituba, East of Tapajos, Para

Bue - Buenavista, Santa Cruz, Bolivia

3. Belem-Panama Transect

BEL -

CUR -

CAL -

Chv - Chaves, Para

Mex - Ilha Mexiana, Para

SEN - Serra do Navio, Amapa (Serra do Navio and Terezinha)

SUR - Surinam, Coast (Paramaribo, Niew Amsterdam, Bigi Santi and Vittijgh)

Tri - Trinidad

Scr - Cumana, Sucre, Venezuela

Arg - Rancho Grande, Aragua, Venezuela

Mot - Motopan, Trujillo, Venezuela

Kas - Kasmene, Zulia, Venezuela

Mar - Santa Marta, Magdalena, Colombia

Nep - San Juan Nepomuceno, Bolivar, Colombia

Ura - Uraba, Cordoba, Colombia (Socorre (Upper Sinu) and Unguia)

PAN - East of Panama, Provinces of Darien and San Blas (Gardner, 1973)

4. Serra do Navio-Pamplona Transect

SEN -

Luc - Lucie River, Surinam

Knk - Kanuku Mountains, Guiana

Ara - Rio Arauca, Arauca, Colombia

Cob - Rio Cobaria, Arauca, Colombia

Pam - Pamplona, Santander, Colombia

5. Panama-Cauca Transect

PAN -

Ura -

Son - Sonson, Antioquia, Colombia

CAU - Valle del Cauca, Colombia (Charguayco, Munchique, Popayan, Rio Saija, and Sabaneta)

6. Pacific Coast

PAN -

Bab - Rio Babahayo, Pinocha, Ecuador

Gua - Guayaquil, Ecuador

Riq - Rique, Eten, Peru

7. Surinam-San Nicolas Transect

SUR -

Luc -

Knk -

Man -

Sni -

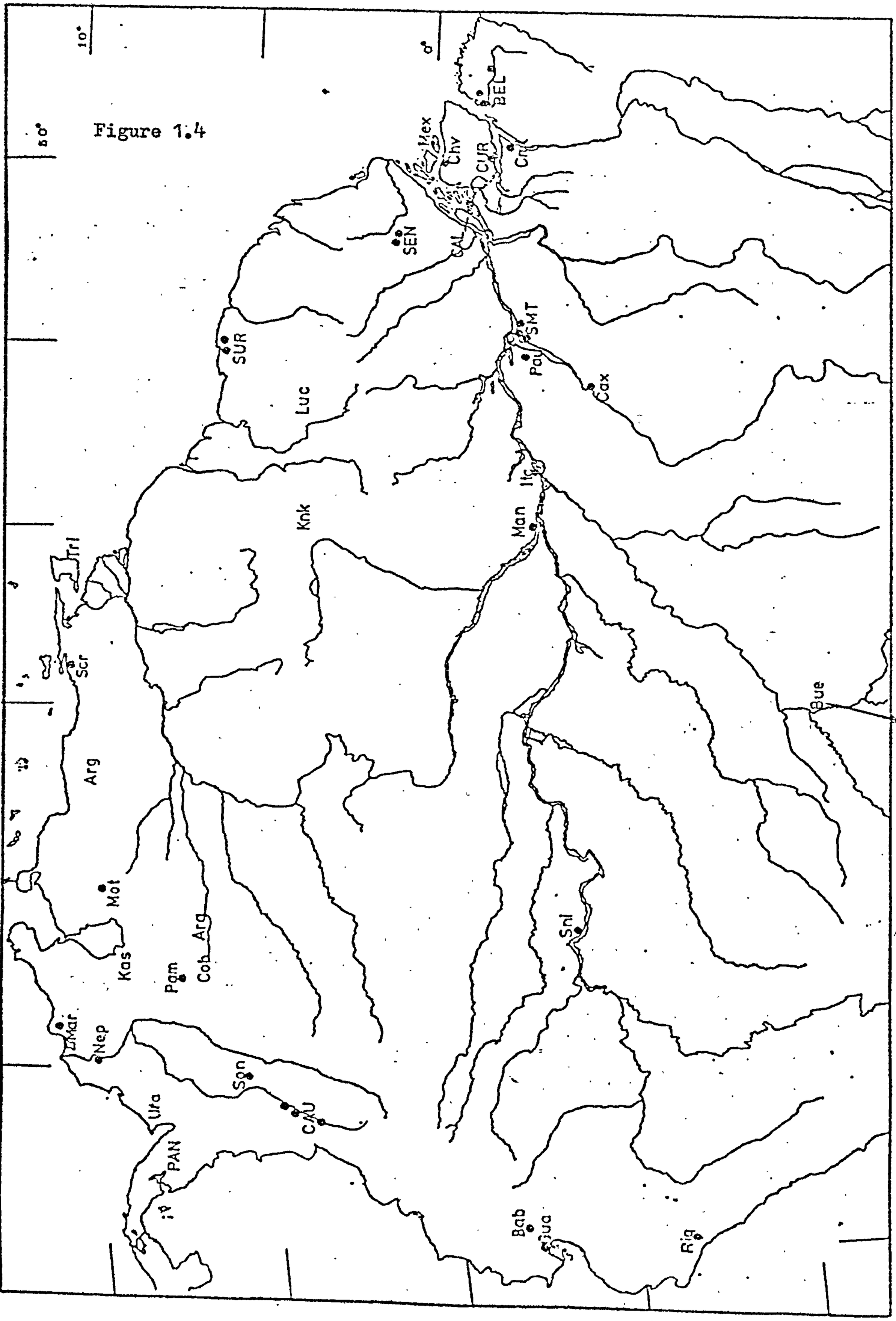
8. Panama-Buenavista Transect

PAN -

Ura -

Figure 1.4 - Collecting localities studied. Northern South America.

Figure 1.4


10°
0°
50
Bel
Wex
Chv
CJR
Cht
SEN
Cal
SMT
Pau
SUR
Luc
Cax
Knk
Man
Trl
Scr
Arg
Mot
Kas
Pam
Coh
Arg
Snl
Bue
Lmar
Nep
Sgn
CAU
Ura
PAN
Bab
Rig

Nep -

Pam -

Cob -

Ara -

Sni -

Bue -

As for the transects of Eastern Brazil, females and males do not share all the localities. Females had no samples from Chv, Cmt Tri, Pau, Cax, Bue, Knk, Luc, Nep, Mar, Bab, Gua, and Riq. Males had no samples from CAL, Scr, Arg, and Mot. The minor sample, Huaf, Huampami in Peru was not located and was inadvertedly ommited. Not all samples have exact locations, only approximations, but all in this case (Figure 1.3) are in such a position that the geometry of the transects is not altered. Again, as for the Eastern Brazil samples, not all samples are major for both sexes. Samples in capital letters represent major ones.

1.3.2 Statistical Methods

The statistics used in this work were kept simple. The methods used came from the usual text-books (Davies, 1971; Edwards, 1976; Simpson et al., 1960 and Sokal & Rohlf, 1969). The data was initially entered in IBM cards, and then processed by computer (IBM 360 and CDC 6600). Some calculations were made with a pocket calculator. The programs were from Davies and Sokal & Rohlf, modified to the present purposes, or by myself.

The basic statistics were first calculated. Then correlations were made between means of localities in order to see the degree of interlocality correlations. Intra-locality correlations

were calculated for the major samples. Characters showing significant values of the correlation coefficient for intra and inter-locality correlations were considered as part of the pleiades and some pairs were taken for regression analysis. Due to the nature of the samples, characters with significant coefficients in all or all but one localities were considered redundant. Unfortunately, the nature of the samples did not allow me to use the method used by Thomas (1968). The small numbers used are such that future research may modify a little bit the result I have obtained. Regression lines were compared by the F test.

The major samples had the differences between their means tested by the Student-Newman-Keuls test. The minor samples were compared along the transects wi h the major ones by *t* test. They were not compared among them. Both the SNK and the *t* were used as Levene's test, as recommended by Van Valen (1978). When along a transect a significant difference was found, a "break" was considered and the analysis did not go further in the transect. The value of *p* in the *t* text was taken into account when the summaries were made. They were considered as well when conclusion was made from the results of these analyses.

CHAPTER II

THE SOUTH AMERICAN LANDSCAPE AND ITS MAMMALS

2.1 INTRODUCTION

Because South America was an island continent throughout most of the Cenozoic, some features of the fauna are unique.

In this chapter, I intend to review some aspects of the South American landscape which seem to be relevant to the history of mammals in this continent.

Some parts of South America have been stable geologically at least since the Cambrian. These areas, the Cratons, are made up of Precambriam rocks. The three Cratons, namely the Guiana Shield, the Central Brazilian Shield and the Coastal Brazilian Shield, as units of South American geology, are stable, positive (with minor localized sub-negative tendencies in Coastal Brazil) and indeformable through the Phanerozoic. In the case of Brazil, the concentration of economic activity on the large areas occupied by these shields has lead Geology not to pay the attention to Paleontology which this latter science deserves. Those areas which have been explored by paleontologists are located in the most prosperous regions which may account for the distribution of the known mammalian fossil localities (Figure 2.1).

Nevertheless, the representation of fossil mammals through the Cenozoic is sufficient to give a clear picture of the history of mammals in South America. There is, however, some uncertainty about relative ages because correlations with the equivalent strata in other parts of the world are not yet well established, and there is some argument about boundaries. The latest revision of South American mammal ages is that of Marshall et. al. (1977) (Figure 2.2).

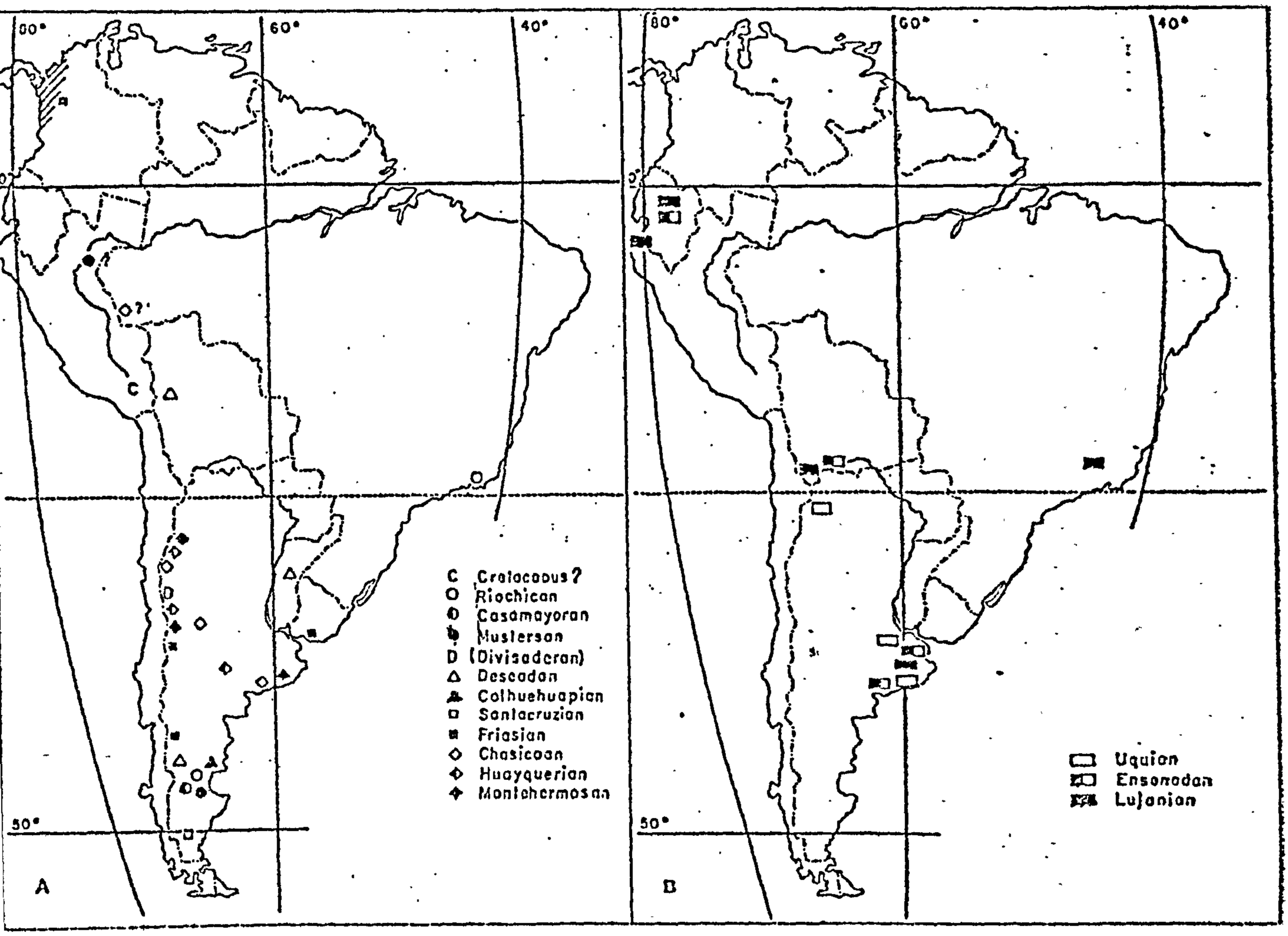


Figure 2.1 - Fossil Mammal Localities in South America. The maps show the areas in South America that have yelded fossil mammals during the Tertiary and Pleistocene. Minor Pleistocenic localities are not shown. See figure 2.2 for corresponding epochs.(After Patterson and Pascual, 1972)

2.2 THE CENOZOIC

Simpson (1948; 1967) and Paula Couto (1952a; 1952b; 1952c; 1953a) presented excellent accounts of the first mammalian faunas of the Tertiary of South America. They demonstrated that the ancient inhabitants consisted of Edentates, Marsupials and several Ungulates.

The Mammal record shows that some kind of grassland vegetation must have occurred. Some authors (e.g. Simpson, 1969; Webb, 1977) have proposed that savana was the predominant vegetation in the early Cenozoic. There is also the proposition that rain-forests covered what is today the Equatorial region. Webb (1977) used the common concept and definition of savana as being "areas covered by grasses and other herbs with scattered trees." The most common savana-like vegetation in South America are the Cerrados where the characteristic facies is caused both by excess aluminium and a lower content of oligoelements in the soil (Arens, 1958, 1963; Goodland, 1971). The concept of Savana vegetation used above could mean vegetation similar to meadows found in Brazil, Argentina and Uruguay, the Pampas, where grasslands are crossed by the fringe forest of the river and lake basins. Trees may also occur scattered throughout the open areas but the soils do not belong to the Pedalfers category as the soils of the Cerrados do. Therefore it is misleading to use the term savana or savana-like in reference to biomes as different as Cerrados and Pampas. To avoid confusion, savana is used here to mean a Cerrados-type of vegetation while grasslands refers to meadows in general.

It is most probable that during the time elapsed between the latest Cretaceous through the Oligocene, grasslands

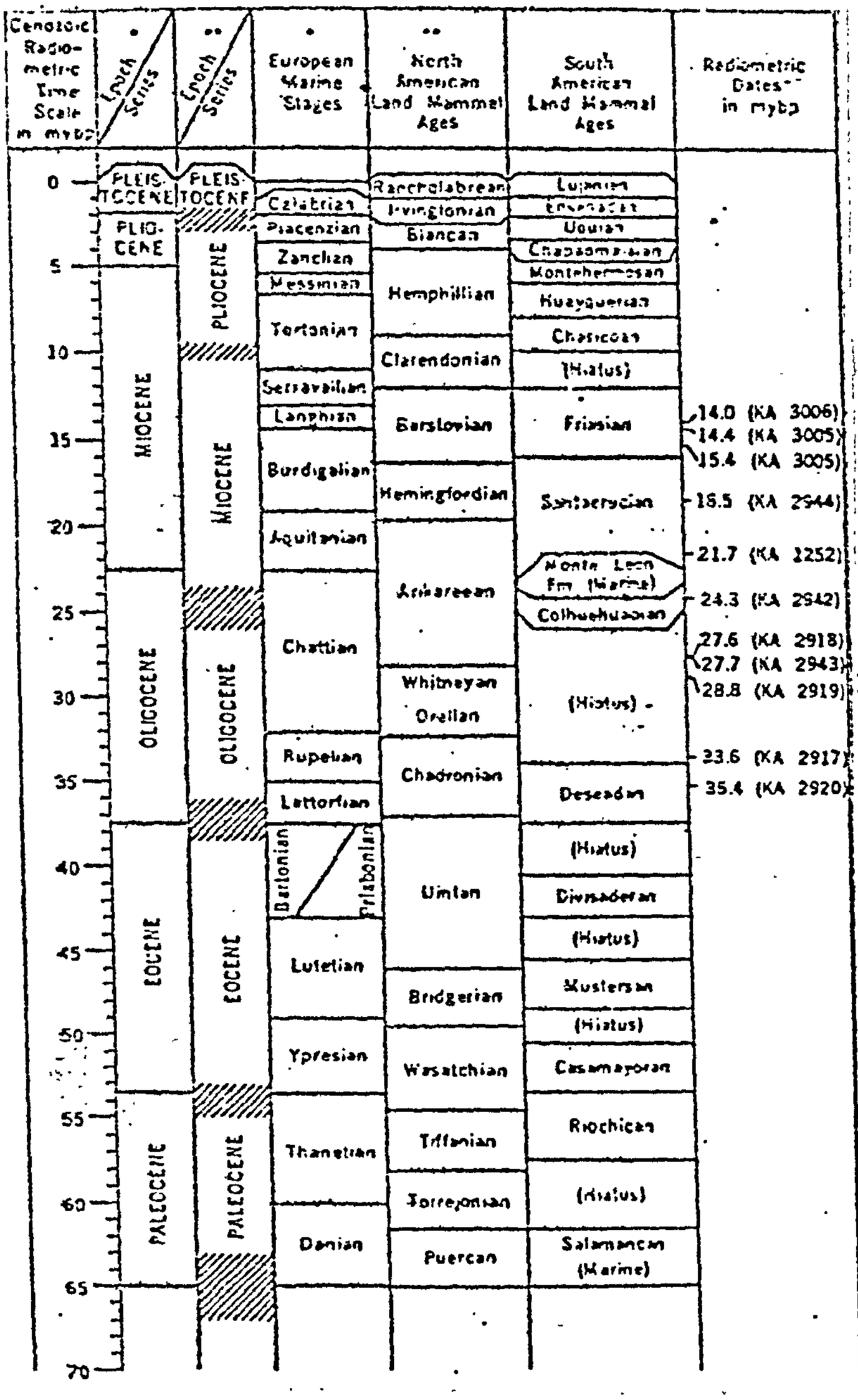


Figure 2.2 - Cenozoic Radiometric Time-Scale and Chronostratigraphy of South American Land Mammal Ages. Correlation with North American Land Mammal Ages and with European Marine Stages is approximate.

mybp, million years before presente.

(After Marshall et al. 1977)

were dominant before the present day types of vegetation and the latter was only to appear with its present features after the Miocene. Hence the Pampas-like vegetation seems to be older than the rain-forest-Cerrado-Caatinga group of related biomes (as they were stated by Veloso, 1966). This group exists in a climate which could originate Pedalfers types of soils, and there is no geological or geomorphological evidence to indicate these kinds of soil were present until the Middle Tertiary.

Forests in favourable regions existed, on the rising Cratons of early Cenozoic and more probably in the slopes of the mountains. Since the Cenozoic began, the continent saw a general orogenic movement both in the Andean region and in the Cratons. There were also several areas favourable to the existence of forests, including primitive rain forests. These forests could be linked through the prairies. The possibility of unknown kinds of vegetation in lower latitutdes is also probable, but since the evidence is so scarce, it is not worth discussing it.(Menendez, 1969; Veloso, 1966).

The geological and paleontological evidence points to the Pliocene as the time when modern tropical vegetational stocks took shape.

The existence of an old sediment in Southeastern Brazil (Bigarella and Andrade, 1965) suggests that the climate throughout the Tertiary was not uniformly humid. The soils were in all probability types belonging to the pedocals group until the Middle Tertiary. The climati fluctuations were not, however, so drastic as in the Quaternary and the vegetation of each region may have remained unaltered for centuries. No truly arid period is recogn-

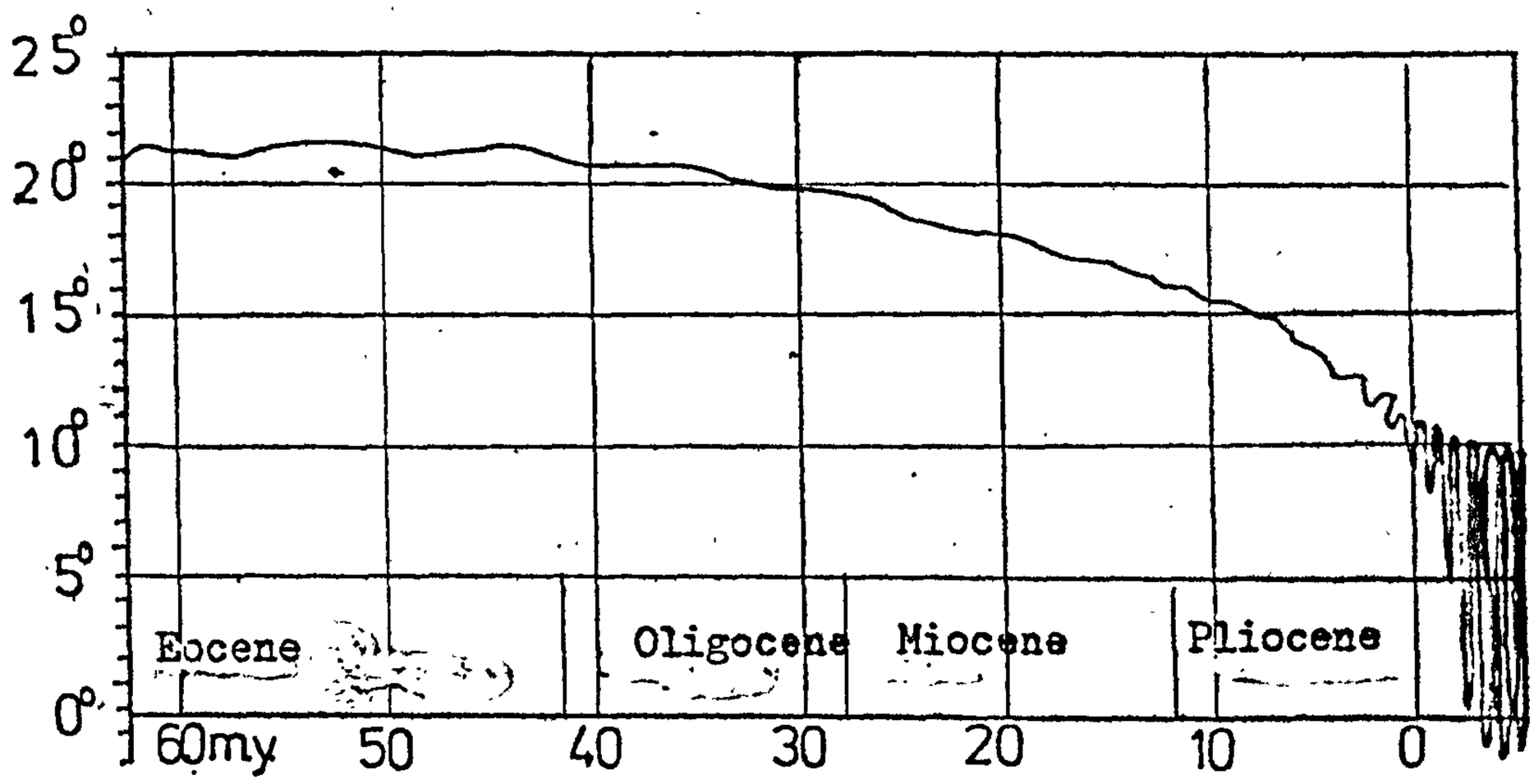


Figure 2.3 - Variation of Temperature throughout the Cenozoic in Central Europe. (After Frenzel, 1973)

izable with certainty and the recorded dry time in the late Oligocene suggests not deserts.but areas with less moisture.

In the Miocene, the first "modern" Marsupials appeared. In the Pliocene Didelphis, Lutreolina, Chironectes and Philander (Paula Couto, 1953b; Patterson & Pascual, 1972; Marshall, 1977) appeared, genera which compose the group of Didelphids with 21 chromosomes (Reig et.al., 1977). Also, the first North American Mammals arrived (Cyonasua group of Procyonids) and this was also the period in which modern vegetation appeared in South America. Several groups of Mammals became extinct during the Pliocene or in the beginnning of the Pleistocene (Borhyaenidae, Sparassocynidae (both Marsupials), most of Litopterna, some Notungulates, a group of Echymidae (Patterson & Pascual, 1972).

The Barreiras series, whose chronology is still uncertain, is, however, frequently placed as being probably Pliocene. Its sediments are of fluviatile or lacustrine origin and in some places are very thick. It is understood that these sediments were formed under a bioclimate of savana (Ab'Saber, 1968).

This period was one of intensive adaptive radiation of Flowering Plants (Ab'Saber, 1968). The major physical feature was the general trend of the climate towards lower temperatures (Axelrod & Bailey, 1969; Frenzel, 1973). It has been suggested that the so-called Ice Age began during the Pliocene (Frenzel, 1973) (Figure 2.3).

The final uplifiting of the Andes took place in this period (Harrington, 1962) and in the Panama region the Panamanian geosyncline was also raised, even though, until the Middle Pliocene, the portal was partially open. The isthmus was completely filled up by the Pliocene/Pleistocene boundary (Haffer, 1970). In some

places the Barreiras series suggests a subsidence in the depression situated among the Andes, the Guianan and the Brazilian shields.

The closing of the Panamanian seaway rendered possible a major faunal interchange between North and South America. It has sometimes been assumed that the invasion by North American mammals caused the extinction of several of the old mammals characteristic of South America. On the other hand, there is an argument about the impact of the newcomers, the intensity of faunal movement, whether these movements were chiefly northwards or southwards, etc. The whole discussion formed the subject of a review by Savage (1974). Reig (1962; 1968; and in preparation) discusses the interactions between the invaders from North America and the old South American fauna. However, it must be noted that these extinctions did not occur suddenly. The majority of them took place in the Quaternary and the invasion of South America occured earlier than that (Reig, in preparation).

"Competition", then, may not be used without reservation as an explanation for these extinctions, at least in a Gausean sense. What, then, happened? The evidence shows that a major climatic change was taking place throughout the formation of the present pattern of circulation of air masses over South American and the spreading of new kinds of vegetation through areas of older vegetational types (Van der Hammen, 1974). Some factors, such as the appearance of new types of soils, impregnated with aluminium and poor in nutrients, may have induced evolutionary changes in living systems throughout the late Tertiary.

2.3 THE QUATERNARY

2.3.1 Introduction

The major features of today's landscape in South America existed throughout the Pleistocene: the general features of relief and the drainage basins (Ab'Saber, 1963; 1971); the basic stocks of today's vegetation and all the present day orders of Mammals. In its beginnings, some orders which will disappear compounded the landscape too.

The chronology of the Quaternary in South America has not been well established. The three Mammal Ages (Uquian, Ensenadan and Lujanian of Patterson & Pascual, 1972), have no absolute dating and are very difficult to correlate with the supposed major climatic episodes which have been studied. Recently, Marshall et.al. considered the Uquian to be the Uppermost Pliocene. The Uquian is characterized by the presence of several boreal elements, Proboscidea, Perissodactyla, Arctiodactyla, Carnivora and Cricetidae (Rodents). This presence has been considered to be the mark of the transition between Pliocene and Pleistocene; then Uquian was considered to be the basal Pleistocene. However, the same authority (Romendo Pascual) who put the Uquian as Pleistocene (1967), now considers it to be Pliocene (co-author with Marshall, 1977). Either way, Uquian can be said to be basal to this epoch.

The following age, Ensenadan had more Boreal Mammals. Several of them attained large sizes. The last age, the Lujanian, had the last showing of several Mammals. Several fossil taxa of this age are stil extant during the Holocene; perhaps the majority of groups of the Lujanian do not differ from the ones of Holocene

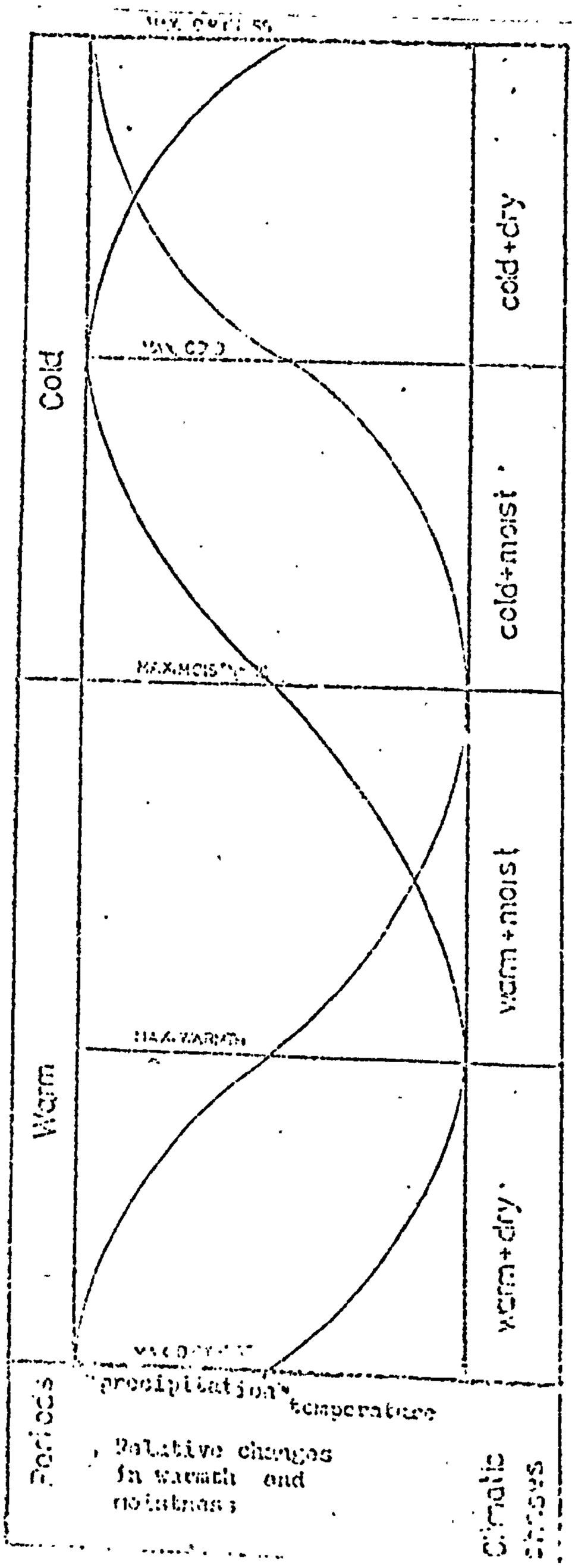


Figure 2.4 - Variation of Warmth and Moistness Through the Quaternary. The thin curve represents precipitation change and the thick one temperature change. (After Frenzel, 1973).

(Pascual et.al., 1967); Patterson & Pascual, 1972; Paula Couto, 1975).

This division of the Mammal ages is not easily comparable with the one related to climatic episodes. Remarks concerning this problem will be made when appropriate.

The climatic trends of the Quaternary were (and probably still are) an alternation of cold and warm periods. Four or five glacial and three or four interglacial plus the Holocene as a last interglacial, are usually considered. Frenzel (1973) considers the possibility that since the Pliocene, the magnitude of climatic fluctuations increased during the Quaternary. The climate changed several times.* Whether or not there were three, four or more cold episodes is not a matter of concern here; in South America there are clear signs that climatic change did occur, and may be correlated tentatively with the last glacials of the Northern hemisphere. There is no direct correlation between these episodes and the ones recorded in South America, excepting for the last one, because there is an absolute dating for it in Colombia (Vuillemier, 1971).

The Quaternary of Neotropics is still very fragmentary and its study is only now gaining momentum. The debate about correlations and other geological matters will not be reviewed here since only the general picture interests us. As Vuillemier (1970) pointed out, the ideas about a stable Neotropics through the Quaternary are no longer tenable as the evidences recently worked out

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*In the above-mentioned work, Frenzel makes a distinction between climatic change and climatic fluctuation, the first being slow, long-term consistent deep alterations in climate, the latter being alterations of a climate with a tendency to reverse or to change directions whether one or several times.

demonstrates that the climatic trends of this epoch have affected South America too. The consequences of these trends is what concerns us here.

2.3.2 Geomorphological Processes and Environments in the Quaternary of Neotropics

There were two sets of processes of geomorphological development in South America during the Quaternary. One set was the processes of mechanical morphogenesis which leads to pedimentary surfaces and the other was the chemical weathering with linear erosion and deep dissection of the terrain. The first occurred during dry periods and the latter during humid ones (Bigarella, Mousinho & Silva, 1965).

Considering these processes, Bigarella & Andrade (1965) avoided the problems caused by small isolated basins with a difficult stratigraphy which have been the bases for the South American Quaternary stratigraphy. They could do long distance correlations with similar landscape which are widespread in Southeastern Brazil.

. The above-mentioned processes are linked also with a kind of vegetational cover, all of which is partially the result of the climate. For instance, during humid phases the areas covered by forests were subject to the rounding of the relief together with an intensive chemical weathering. The forest protects the soil against aggressive erosion. In dry phases, with the retreat of forests, the areas were subject to pedimentation, i.e. to the formation of sloping erosional plains at the feet of mountains or in valleys (Ab'Saber, 1971; Bigarella and Andrade, 1965).

If these assumptions are correct, as they seem to be, then it can be postulated that during some periods, the forests were widespread and in others, other forms of vegetation occured there instead. At the same time, it must be emphasized that although this is the general picture, the situation in each area differed due to the continent's zonation which is disturbed by the Andes, hence the emergence of particular cases.

Another important point, is that the idea of correlating glacial phases with pluvials (e.g. Moreau, 1963; 1966) seems not to be correct. Bigarella et.al. (1965), made the point that the studies on the Brazilian landscape seem to agree with the hypothesis of high humidity correlating with interglacials while semi-aridity with glacials. I tend to agree with these authors and I think the picture is more probable as expressed in fig. 2.4, where increasing cold corresponds to maximum humidity. However, when there are large ice sheets covering large areas and the glaciation rises towards its peak, the humidity decreases, thus the dry period coincides with glacial maxima. The effects of deglaciation causes the inversion of the humidity curve which then rises towards its peak, although very hot times might not be favourable to high humidity. Anyway, the curves are not so clear cut, climatic fluctuations occuring between glacial maxima and interglacial maxima.

2.3.3 The Vegetation of South America

1. Characterization of the vegetation

Several methods have been suggested to characterize a vegetation. The resulting classifications from these methods

are all debatable, and a zoologist has a difficult task in choosing the one which is most appropriate to his own needs. However, the present knowledge ensures that one can rely, to a certain extent, on some "natural regions" of the geographer. For instance, the names "Pampas" or "Caatinga", when used correspond broadly to recognizable geographical regions, with some homogeneity in ecological terms.

The majority of vegetation classifications are based on floral accounts, physiognomic features and, sometimes, on phytosociological studies. Few have been made by a combination of these aspects. At the same time, the physiography of the areas concerned are superimposed on the classification obtained. Since these physical factors determine the very existence of a given vegetation, the classification which exists today generally corresponds to "natural regions".

The major shortcoming of most existing classifications is the typological thought which underlies them. As idealistic approaches there are discrete borders between the recognized formations, even the best systems used have this problem (e.g. Cabrera & Willink, 1973; Hueck, 1972; Veloso, 1966). The resulting systems are synchronic, concerned not with ecosystems (generally speaking, but see Veloso, 1966, for an ecological approach) but only with vegetational formations. Intermediate types are seldom recognizable and community evolution is not part of the systems. When analysisng the geography of evolution, the student interested in the changing environments must use an epicycle-type of reasoning to acquire the informational content of the vegetation.

As I said above, not all the schemes which have been

proposed recently have this characteristic. Ab'Saber (1971;1977a) developed one approach to the natural spaces in South America which, instead of classifying the vegetation and then correlating the physiography and faunations with it, departs from the set of biogeographic physiografic and ecological features. He found that the core area of all of thexe factors form a nucleus. These nucleus areas are the Morphoclimatic Domains. The idea of a changing environment is also incorporated in the argument (1977b). Of course the whole idea is very new, with several problems in its application. However, when a zoologist considers the large scale phenomena of evolution, the short-comings are few and of minor importance when compared with other approaches. The detail is sometimes important. However, as Vanzolini correctly pointed out (1970) a very fine classification is not always convenient, either because it is irrelevant or because there is not enough data for its use.

The areas in South America as far as terrestrial vertebrates are concerned can be divided into three major types: the open areas, the forest areas and the oreal areas. These areas function sometimes as large aggregations of several morphoclimatic domains. For example, The Caatinga, the Cerrados and the Chaco (with the intermediate belts between them included) together form a very large continuous open area in which vertebrates occur, sometimes in a continuous fashion. (Vanzolini, 1970; 1976). The name applies to the forest domains of the Araucaria uplands which is continuous with the Tropical Atlantic domain. Another example is the oreal domains in the Andes. However, for each taxon an anlysis even when it takes into account this general type, must take into consideration the particularity of the group.

At the same time, zonal and topographical influences exist in these areas (and of course an area such as these has several morphoclimatic domains due to these very reasons), and generalizations must be cautious.

2. Morphoclimatic domains, enclaves, dynamics of biogeographical change and their use.

The Domains are broad ecological systems in South America today. The history of the whole continent must be taken into account when understanding the geography of evolution. The domains have little to do with Geology and are very sensitive to climatic changes. These changes and fluctuations alter both the picture and the previous distribution of the domains or in more rigourous terms the approximate localization of the natural domains in the past.

Inside the domains there are often enclaves of different vegetation, which are related floristically with a domain outside the one in which the enclave is found. Other enclaves are edaphic forms with difficult correlations. The analysis of these peculiar vegetations clarifies the very nature of the landscapes which are continuously changing.

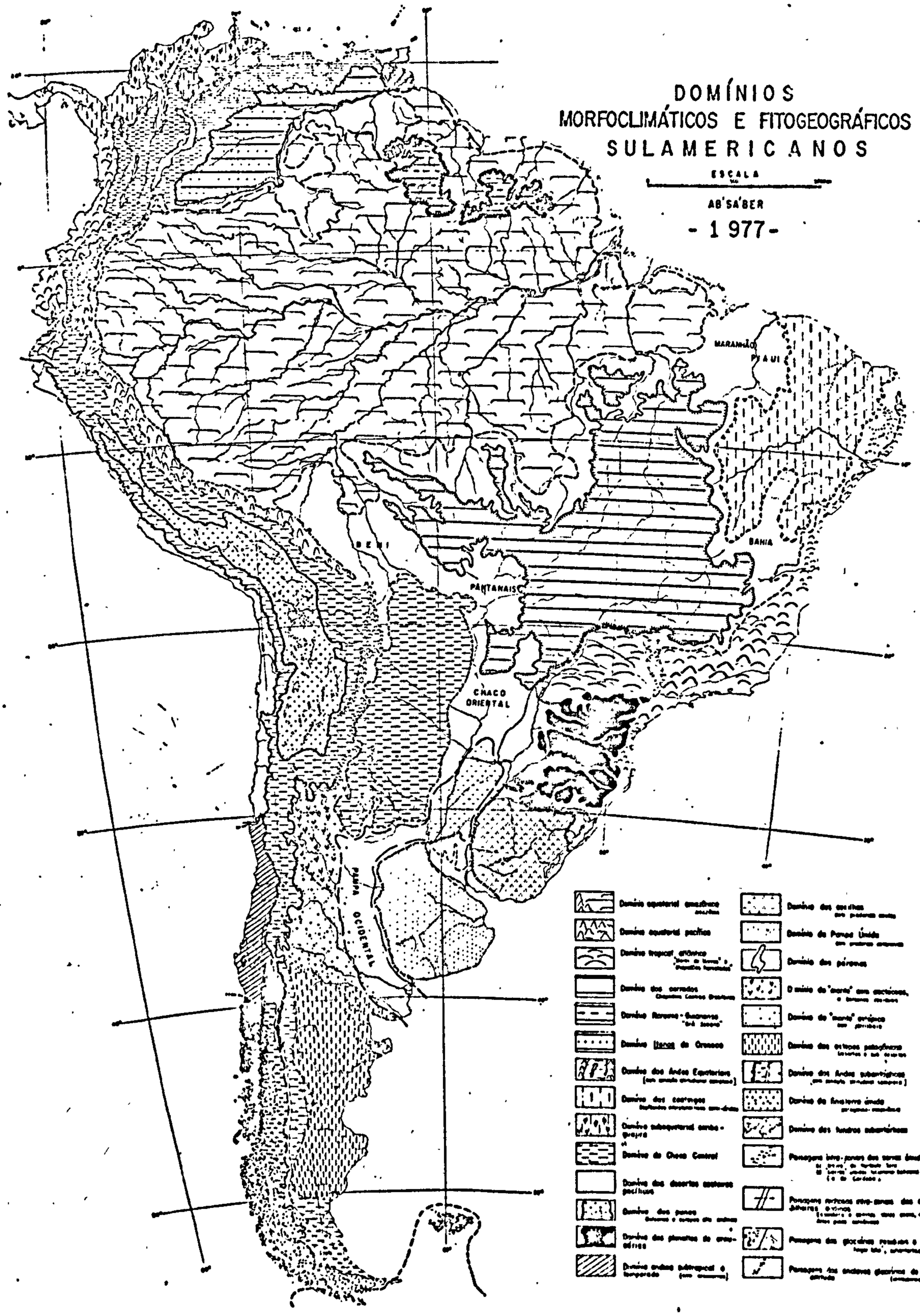
The vegetational stocks found in South America, and their complex inter-relationships are a Quaternary phenomenon. As discussed above, during the Cenozoic, different types existed and during the Pliocene the floristic and faunal stocks appeared. If this postulate is correct, the analysis of Pleistocene changes in fauna and flora of South America can be made with little regard to its predecessor. The term with little regard is used because

some vegetations are older than Pliocene. One example could be the Northern Monte Domain where the vegetation perhaps came from a Cretaceous stock. Pliocene is both the end of the Cenozoic and the beginnings of the Quaternary's formation, and long range trends of the patterns of life are to be found in their beds.

An analysis of the geography of evolution of a particular taxon can be made in two phases, analysing the distribution of the taxon concerned, first in relation to the morphoclimatic domains and second to the dynamics of the landscape during the Pleistocene. However, the amount of data and its interpretation which could give a picture of the past distribution of the domains is small and is only available for the uppermost Pleistocene. Even that can be very misleading when an inadequate conceptual scheme is used (e.g. Hester, 1966).

From a Zoologist's point of view, the delimitations of the domain in South America is the best help the geographer can give to him. In recent years, a wealth of new interpretations of vegetational patterns of this Continent have appeared. Some modern syntheses are now available (e.g. Veloso, 1966; Hueck, 1972; Cabrera & Willink, 1973) and are valuable and sensible sources. However, it is difficult to use these sources directly, and even more detailed ones, such as the RADAM project maps (see under BRASIL in the bibliography) because the majority of zoological collections have specimens without any precise indication of locality. Sometimes one can not even find the place written on the label. As a result, because the use of domains, with their less precise boundaries, is nevertheless potentially more informative, I shall use this conceptual framework here.

FIGURE 2.5


DOMÍNIOS
MORFOCLIMÁTICOS E FITOGEOGRÁFICOS
SULAMERICANOS
ESCALA
AB'SA'BER
- 1 977 -
MARANHÃO
PIAUI
BAHIA
PANTANAIS
CHACO ORIENTAL
PAMPA OCIDENTAL
Domínio equatorial amazônico
Domínio equatorial pacífico
Domínio tropical atlântico
Domínio dos cerrados
Domínio Roraima - Guianense
Domínio Hileia de Orenoco
Domínio dos Andes Equatoriais
Domínio dos caatingas
Domínio subequatorial semi-árido
Domínio do Chaco Central
Domínio dos desertos costeiros pacíficos
Domínio dos pampas
Domínio dos planaltos de araucárias
Domínio ombro subtropical e temperado
Domínio dos cerrados
Domínio da Pampa Úmida
Domínio dos pântanos
Domínio do "morro" com elevações
Domínio do "morro" arredondado
Domínio das estepes patagônicas
Domínio dos Andes subtropicais
Domínio da floresta úmida
Domínio dos tundras subantárticas
Pantanos intra-zonais das zonas úmidas
Pantanos perenes intra-zonais das savanas
Pantanos das glaciais recuados e
Pantanos das costeiras desérticas de

What characterizes a morphoclimatic domain is the superimposition of some typical geographical features of relief, climate, hydrology and vegetation. With this method core areas appear and they may be characterized by their typical vegetation. Between the core areas there are more or less broad transitional belts. In the core a chief major vegetation formation is to be found, but, although dominant, these formations are not exclusive either due to the existence of large enclaves of different vegetations or to the edaphic forms which occur scattered throughout the domain.

Twenty-seven domains are recognized (Fig. 2.5) A brief characterization is given in appendix I, chiefly the ones concerned with the South American portion of the Brazilian sub-region of Neotropics (in Hershkovitz! 1969, 1972, sense). The classification is by Ab'Saber (1977a and 1977b) where the theoretical bases for the present approach can be found. The vegetation is taken as the major typical feature. Therefore the domains will be called, in general, by the name of their major vegetational formations. Sometimes however, a well-known geographic name is used instead. When necessary, the proper geographic names considered by Ab'Saber (1977) are given in brackets.

2.4 VEGETATIONAL CHANGE

The botanist regards clima as the major environmental factor determining the distribution of plants. However, together with the macroclimate soils as well local meso and microclimatic factors will be responsible by the shaping of this distribution. For large vegetational formations climate is undoubtedly of chief importance. The morphoclimatic domains (Fig. 2.5) assumes for each

major biome a particular interaction of climate, soil, orography as well as vegetation.

On the bases of geological knowledge, it can be postulated that the major physiographic features of South America have been stable during the Pleistocene. The climate has fluctuated and changed during all the Quaternary. Thus it is expected that the arrangement of paleo-spaces during this period has been different in the past. If this assumption is correct, it is possible to reconstruct the vegetational distribution of the past. If only the present relationship of climate and vegetation is taken into account, a falsifiable picture will appear. For instance, Hester (1966) proposed an arrangement of the past vegetation during the last glacial maximum which is unlikely. He considered the possibility of existence of Araucaria in Roraima region. The occurrence of this type of vegetation in this place must have followed a dispersal throughout rain forests, cerrados, etc. This possibility is, for instance, very unlikely whereas the Araucaria would have had to cross all the way by chance dispersal in order to colonize areas already occupied by other plants, then compete successfully for the space, etc. Simple reasoning rules out this reconstruction. At the same time, evidences exist for a permanence of arid conditions in Northeastern Brazil during this period. But in this region, his reasoning would lead to the placing of a rain forest!

This kind of reconstruction is based on the assumption that changing temperatures correspond directly to changes in vegetational distribution, which will correspond for each place with a temperature:where today certain kinds of vegetation exist, these places will see the extension of the same vegetation.

The climatic and vegetational history of Neotropics is not fully known or understood yet. To make maps showing the sequence of landscapes through the whole Pleistocene is not possible as yet. However, I think the reconstructions already made for some periods and chiefly for the last climatic phases are possible.

2.4.1 Vegetational and Climatic History

Southern South America has a record of Pliocene glaciation (Mercer, 1975). During the Pleistocene a number of glaciations were restricted to the Andes, nowhere else being affected. Some authors think glaciation occured at Itatiaia Range, Serra da Mantiqueira (Vuilleumier, 1971 and references in this article).

When glaciations were occuring in the higher mountains the temperature was probably low in the rest of the continent. Together with other climatic factors which were also altered, the cold periods determined changes in the arrangement of natural spaces, changing vegetation and faunation.

The graudal uplift of the Andes, a changing climate, the establishment of the Panamanian terrestrial route have been factors favouring the emergence of new taxa throughout the Pleistocene.

Palynological analyses performed in cores from the Colombian Andes evidence a dominance of tropical elements in early Pliocene. With the upheaval of the Cordillera in late Pliocene, polen characteristics from the Paramo arise. The elevation of the Andes was then high enough to allow the emergence of this kind of vegetation. The dominance of the Paramo at the altitude in which its elements occured indicates an early cold phase. The Paramo and

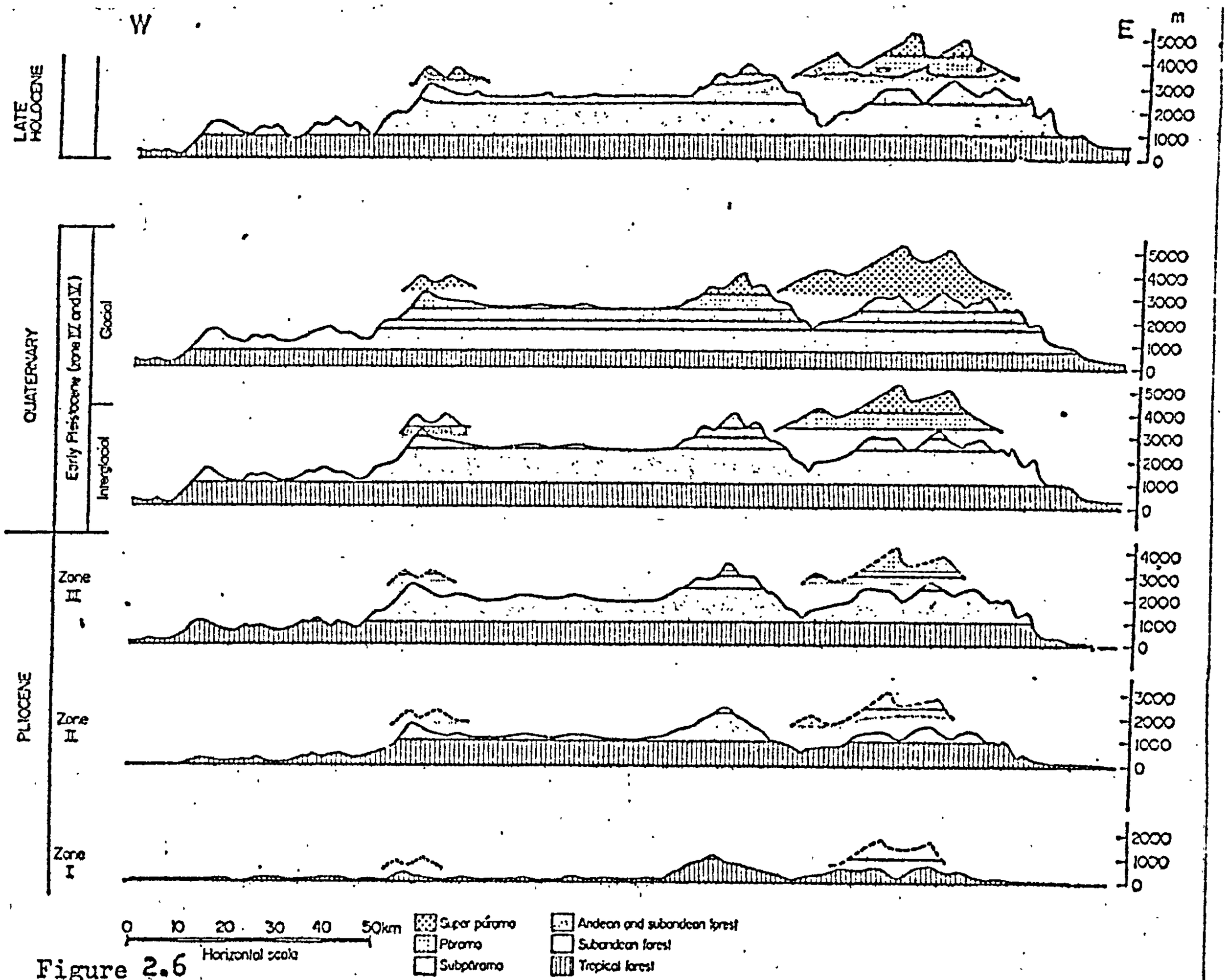


Figure 2.6

Sections through the Cordillera Oriental (Colombia) showing tentative reconstruction of vegetation belts during the successive stages of uplift and during an early Pleistocene interglacial and glacial. The uppermost section shows the present situation. The main section is east-west at the latitude of Bogotá. The small sections above each section are from higher areas further to the north. (Van der Hammen, 1974)

the Andean Forest below were poorer in species than they are today. Boreal elements as well as ones from the forest apparently invaded the new heights to form the Paramo. New kinds of plants appeared and the Quaternary pattern took shape. Van der Hammen and colleagues (1973), who performed the palynological analyses, interpret the data as an invasion of a new unoccupied habitat, the high altitudes of the Andes. Boreal elements came by chance dispersal through the Panamanian route. Continued uplifiting and climatic change linked and separated continuously the Paramo "islands", favouring speciation processes.

These processes explain the diversity of present day landscape. When a biome is split into "islands", population gets isolated and geographical speciation may occur (Mayr, 1942; 1963). When the isolated populations came in contact again, some of them may have been differentiated in such a way thht, even potentially inter-breeding ones could have had character displacement (Brown & Wilson, 1956). Character displacement is considered to be a mechanism to avoid competition, competitive exclusion and to "fill" "empty niches" as well. Vanzolini has suggested that during the South American Quaternary, such mechanisms could have occured extensively (Vanzolini, 1970).

The polen diagrams obtained by Van der Hammen's team, tell a history of recurrent climatic change throughout the Pleistocene and Holocene (Figs. 2.6 and 2.7). Data of the same kind from the Guianan coastal lowlands and inland savanas (Van der Hammen, 1963; Wijmstra & Van der Hammen, 1966) as well as from the Amazonia, also provides further evidences of changes in climate and vegetation.

The late Pleistocene has a more detailed set of data.

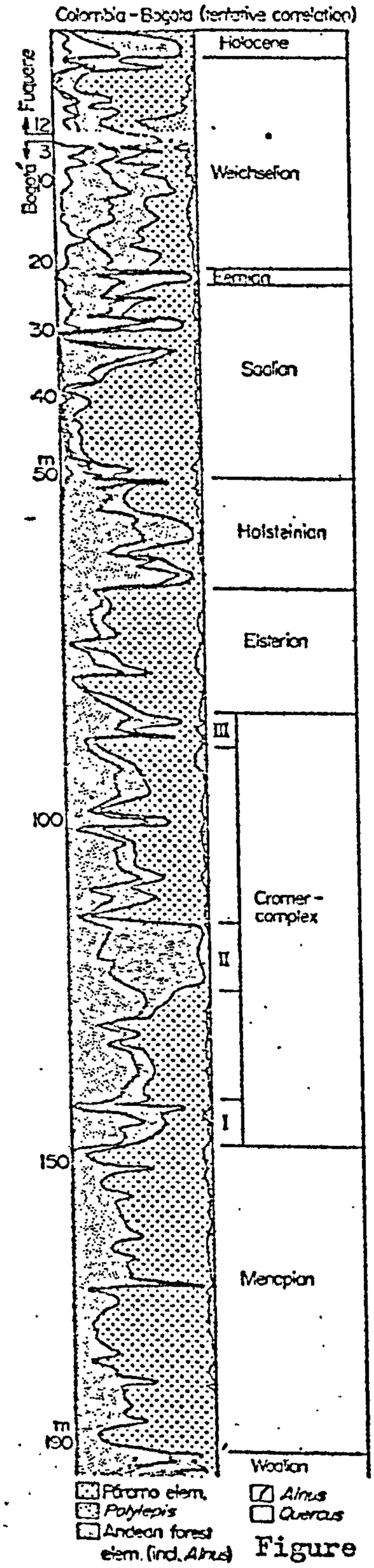


Figure 2.7

Pollen diagram of c. 200 m lake sediments from the high plain of Bogotá (section CUY); the uppermost part is from Fuquene. The European chronostratigraphic names are only tentatively used.

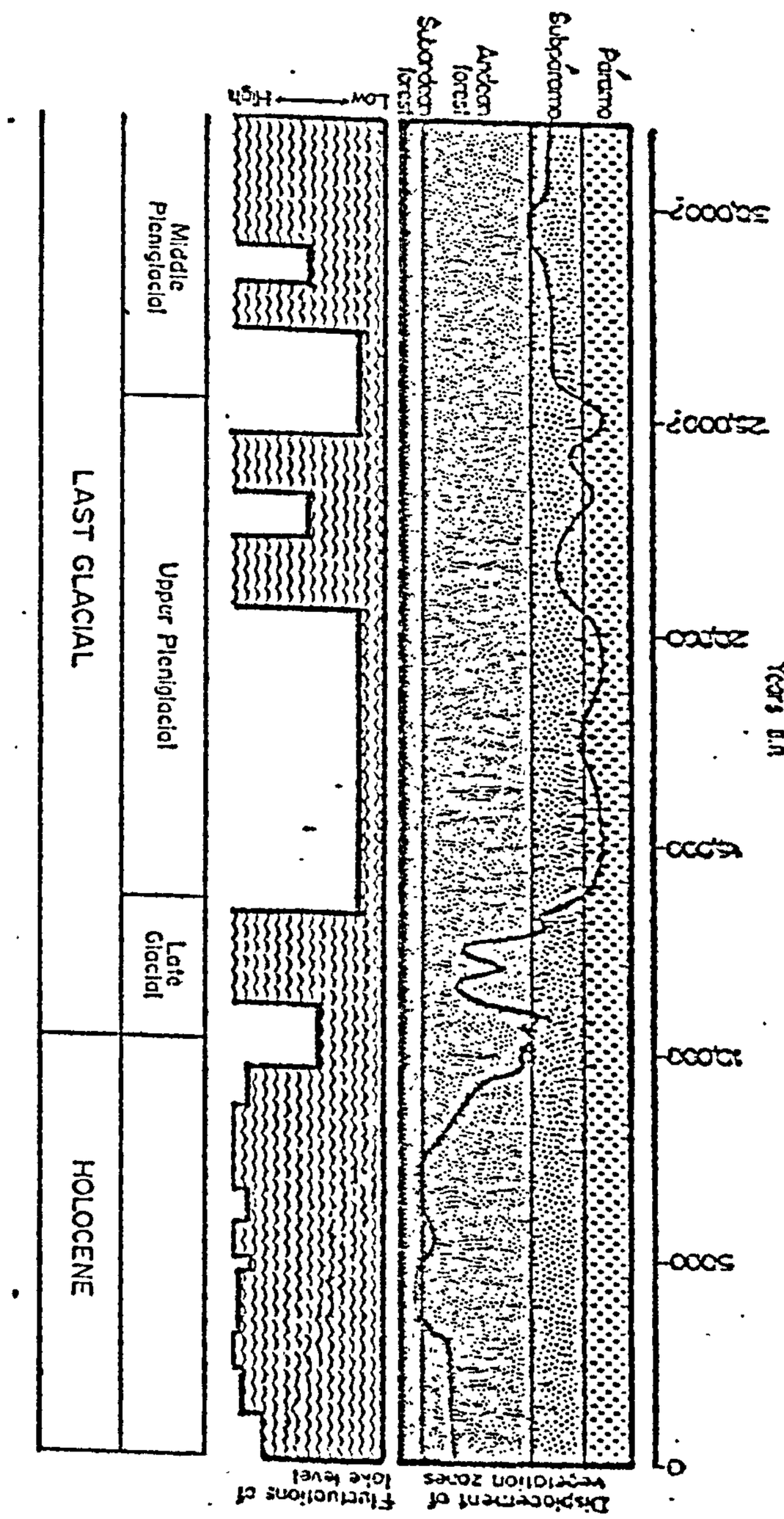


Figure 2.8

Displacement of vegetation zones and fluctuations of lake level, Laguna de Fuquene (see diagram Fig.. (Adapted from Van Geel & Van der Hammen, 1973.)

The lake sediments from Bogota and Fuquene (Figs 2.7; 2.8) indicate that the penultimate glacial period was very cold and dry. The last interglacial was warm, perhaps warmer than it is today. The last glacial had a moist condition at first. During the last pleniglacial it was much colder, its coldest phase starting about 26000 years ago. The data suggests fluctuations until 21,000 years, when a very cold and dry phase began. During the time between 32,000 and 21,000 years ago, approximately, the general trend was the increasing cold, with some dryer periods, judging from the lake level of Laguna Fuquene (Fig 2.8). After that, the cold period continued with a very dry climate (Van der Hammen, 1974).

The cold/wet climate probably favoured the spread of the Andean vegetation throughout large areas of the continent. "Andean" elements are found within the Flora of the Araucaria domain. Terminalia triflora, for instance, is a tree found in the Ilha de Santa Catarina, which is presently in the Atlantic Domain, and in the Tucumana-Bolivian forests (Klein, 1975). In the caves of Lagoa Santa, State of Minas Gerais, a fossil mammal fauna is known. Paula Couto (1975) attributed it to the Lujanian, i.e. uppermost Pleistocene. F.L.S. Cunha (personal communication) thinks the sediments from one cave in the area have been deposited during the last 20,000 years. The Araucaria domain has also an "Andean" Cricetid and some invertebrates of the same "origin".

These data suggest that the vegetation which is today restricted to the Andes existed in the past in other areas of South America. The structure of communities in the Araucaria region led Klein (1975) to assume that the present vegetational structure was preceded by others. The same structures led one to assume the events related with them as having occurred in the recent past

lets say before the ultimate glacial maxima. Probably during the late pleniglacial, lower temperatures and high humidity allowed links between the vegetation of the foothills of the Andes and the Brazilian uplands between 20° and 30° latitude South approximately.

Some areas of the Chaco remained dry, since local variations of rainfall today, as in the past, determines the existence of deserts in some areas and in others, some kind of forest vegetation. The other arid regions, the Monte, the Caatinga, the Pacific Coastal Desert, the Guajira, had their area reduced too. For instance, the Caatinga may have been reduced to a strip around 36° West of longitude and in the plateaus, the gallery forests enlarged and the Brejos increased in area, linking the Atlantic forest with the Amazonia.

Some parts of the Central Brazilian Highlands may have had forests as well. However, Cerrados may have remained scattered through these forests, and a large Cerrados area probably existed (Ab'Saber, 1971; 1977). The Araucaria existed in the Serra do Mar and Serra da Mantiqueira in a more continuous fashion than today, entering in the highlands of Minas Gerais as well.

The present disjunction of Araùcaria in the Andes and Southern Brazil was probably due to an event prior to the Upper Pleistocene. Some links between the Southern and Northern Andean forests may have existed, but is more unlikely, since the floral elements in Southern Brazil are more linked with Tucumano Bolivian region.

It will be necessary to make more studies to complete and correct this picture, although it is a very probable one.

Following this period increasing aridity changed the patterns. As in the preceding period, the same stocks of vegetation participated to shape the landscape which corresponds to the last glacial maximum.

Ab'Saber (1977b) summarized the present status of knowledge in a map (Fig 2.9). A large amount of sedimentological, geomorphological and ecological data was used. The general mechanism which explains the occurence and distribution of different climate in South America was discussed by Damuth and Fairbridge (1970). During the Wurm period, the Caatinga expanded, penetrating in areas which are now Cerrados and forests. Cerrados and other savanas occupied large areas throughout Amazonia, getting connections between Cerrados, the Gran-Sabana and the Llanos del Orinoco. A large area in the central highlands of Brazil remained covered by Cerrados while xerophytic vegetation occupied the Northern highlands as well as the peripheric and interhighland depressions. The widespread existence of Caatinga-like vegetation divided the Cerrados even in Amazonia. The Cerrados got reduced as a macroenclave in its nuclear area (Ab'Saber, 1977b) Fig. 2.9)

In the Amazon basin the forests were restrited to areas, large and small, which functioned as refuges for vegetation and fauna. Along the river banks, gallery forests probably existed. Ab'Saber believes that in some areas even the Caatinga penetrated. The basin was a mosaic, dominated chiefly by Savanas notched by gallery forests with some peripheric semi-arid vegetation and with refuges of forests, some of them rather large, where local conditions allowed. What today is the exception -the transitional belts

FIG. 2.9

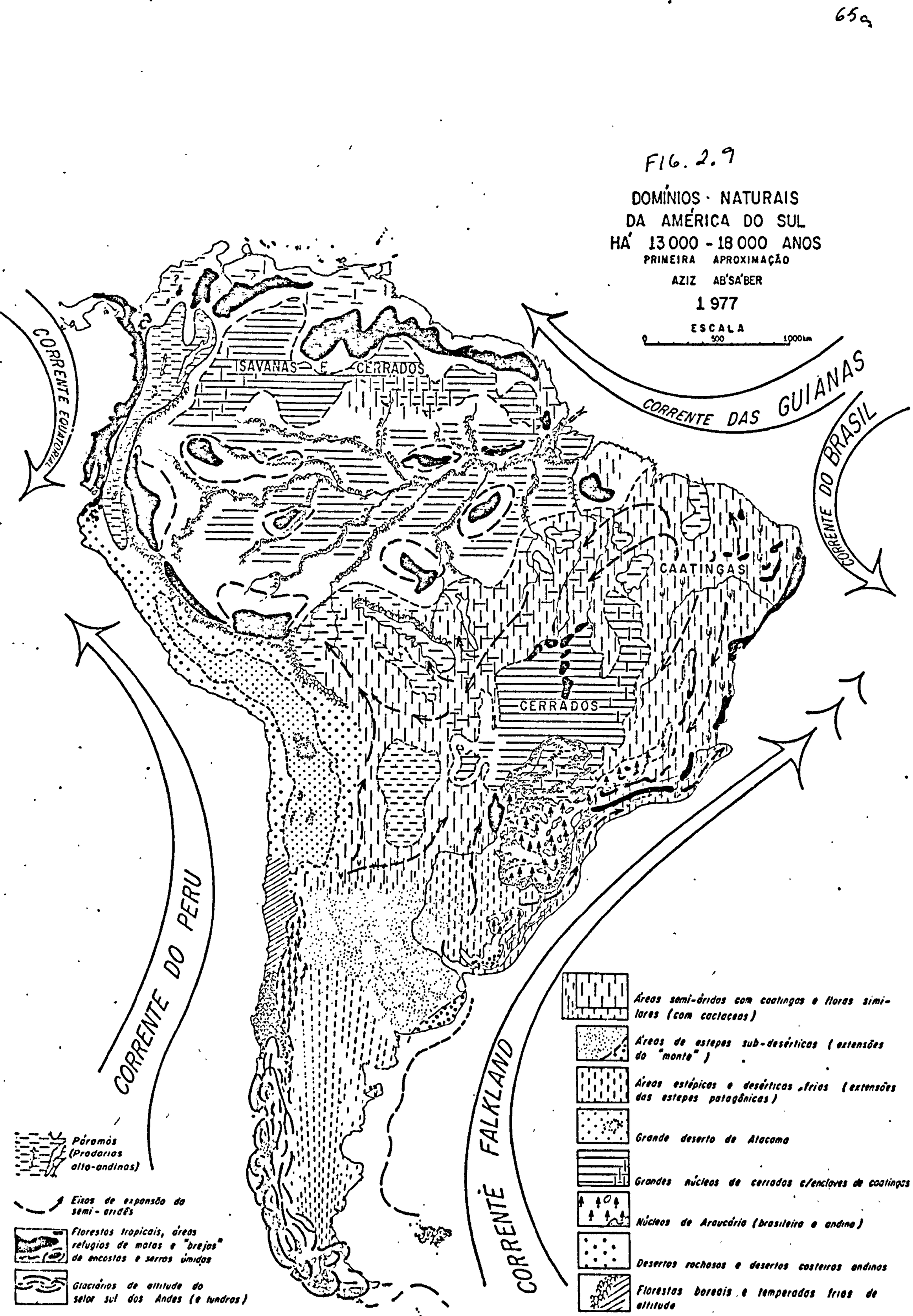
DOMÍNIOS · NATURAIS DA AMÉRICA DO SUL HÁ 13 000 - 18 000 ANOS

PRIMEIRA APROXIMAÇÃO

AZIZ AB'SA'BER

1 977

ESCALA 0 500 1000 km



Des.. Hélio

betweem tje dp,aoms- during the Wurm was more widespread, complex transitional areas.

In the Andes, the glaciation lowered the snow-line and all the zonation was lowered as well, the Oreal open areas being connected (Van der Hammem, 1974). In general, the majority of open areas came in contact with their next neighbour. As at times, the neighbour was an arid vegetational formation, it can not be said that all open areas were connected in a way that free pass could occur for all organisms.

The Araucaria forest was probably less dense, but this Conifer expanded its area to where local conditions of moisture allowed it, even in the poor Cerrados soil, since Araucaria grows usually in poor soil (M.B. Aragao, personal communication). The scattered population of it northward in Sao Paulo today, are residuals of the former expansion.

The arid phase caused the invasion of the more homogeneous domains which exist during humid periods by the transitional vegetation. There was a substitution of the domains by complex mosaic, open areas predominating. This is in strong contrast with the humid and cool periods when open areas were probably reduced to small patches scattered through predominantly forested landscapes. The Cerrados in as much as the Caatinga, i.e. the savanas and semi-arid open areas, remained with somewhat large core areas.

The Holocene saw the increase of temperature and humidity. The early Holocene may be visualized as having an organization of South American natural spaces similar to today's. The recurrence of cold/dry climate occured in the Holocene. During this period, the climate flcutuated. Fairbridge (1962) made a curve of the fluctuations of sea-level which is understood to be

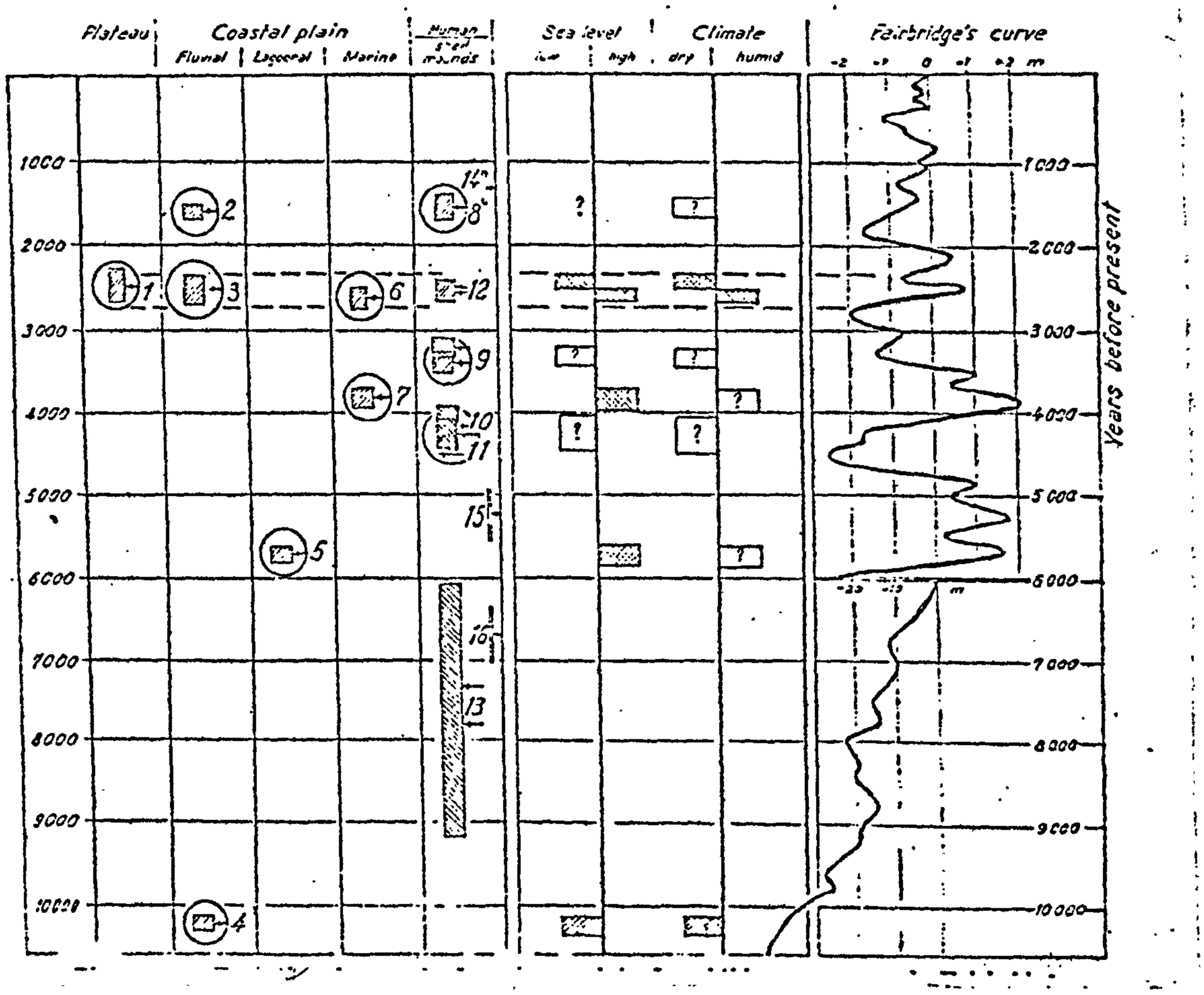


Figure 2.10 - Tentative Correlation between Brazilian Holocenic Datations and the Fairbridge's Curve (Bigarella,1971)

correlated with variations in the climate (Fig 2.10). The lowering of sea-level is explained as a result of an increase of the ice sheets in the glaciers. An increase of temperature means an increased ice thaw and the lowering of temperatures increases the incorporation of water as ice in the glaciers.Thus the variation of sea-level.

The curve can be seen as a general indicator of recent climatic fluctuations. Even if debatable, this curve has a high explanatory content and can be considered to be a guide for understanding the climatic instability.

Radiometric datations from holocenic localities in Brazil have been correlated with the Fairbridge Curve (Fig. 2.10), (Bigarella 1971). In these localities, paleosoils, dunes, sedimentary sequences and terraces in river banks were analysed in order to establish what climatic conditions prevailed during their formation. Afterwards, radiometric datations were performed. The results (Fig 2.10) are roughly comparable with the Fairbridge curve. These data indicate that the fluctuations of climate during the Holocene was probably very intensive, leading sometimes to rigorous climates. Unfortunately, no polinic analysis has been performed in any of these localities.

When the Fairbridge curve is visually compared with the palynological data from Northern South America, it is apparent that the holocenic fluctuations were not so intense as the variations of climatic change. The climate in Holocene never reached the peaks of humidity or aridity as in the Pleistocene. However, all the available data indicate an arid phase between 5000 and 4000 years ago, and another between 3000 and 2000 years ago, the latter being less severe than the first. Even if these changes were not so severe as the last glacial maxima, they had effects upon the distribution of organisms. In the future, more date will be needed from other regions

in order to establish more precisely what the extent and influence of these fluctuations had been. All data suggests an environmental change all the time. The changes were in everything, temperature, rainfall, cloudness, and consequent insulation, etc. Damuth and Fairbridge (1970) demonstrated also that changes occured in the pattern of air masses circulation and oceanic streams.

For the organisms, the pysical environment is in perpetual change. To follow this changes, evolutionary modification occured and the communities changed all the time, not only in terms of a real distribution, but in their structure as well.

2.5. THE DYNAMICS OF PLEISTOCENIC AND HOLOCENIC CHANGE IN SOUTH AMERICA

There is a wealth of information concerning the past landscapes of South America. The evidence shows a continuous transformation in the landscape which can be seen as a result of changes in the climate during the Pleistocene and Holocene. These climatic changes are roughly correlated with European and North American Ice Ages (Bigarella & Andrade, 1965). Glaciations appear to have occured only in the Andes: extra-Andean regions in the South and elsewhere were not covered by ice sheets (Polansky, 1965). However, the overall climate of the continent did change.

The oldest known glaciation seems to have occured about 3.5 Mybp in the Pliocene. The history of glaciations is not well-known, apparently the last one was the largest and obliterated the evidence about former ones (Polansky, 1965). In general, the dating of the most recent climatic events (from 40000ybp onwards) is in agreement with climatic events elsewhere. From the last

glacial to the Holocene correlation between south and north, hemisphere events can be made by absolute dates by C^{14}.

Changes in vegetation in the Northern Andes have been well recored and show an interesting picture from the Pliocene through the Holocene. However, the present knowledge on the subject is for the most part, not extensive. The large Brazilian portion has few fossils recorded from the Tertiary/Quaternary and Brazilian geologists are trying to work out the stratigraphy of the region aided by geomorphological features. Ab'Saber (1971) considers that the fast erosion which resulted from the alternation of dry/wet phases destroyed most of the old Tertiary sediments.

The mammals have been located in the Quaternary in two ages (Marshall et.al.,1977). As several major climatic events occured it is difficult to correlate them with these two distinct faunas. The Lujanian, latest mammal age, may however be placed as upper Pleistocene, the time of the last pleniglacial. The Lujanian fauna contains in both Brazil and Argentina, an assemblage of some modern genera, some extinct ones, and some which are relatives of modern ones. The fauna of the caves in Brazil is considered to be of this age.

The problem which arises when one tries to interpret the present distributional patterns in terms of past events is that the evidence diminishes as one goes back in time. Processes which occured in one period frequently destroyed the evidence of the previous one.

However, since it can be demonstrated that the distribution of biomes varied, that the basic stocks of both mammals and vegetation began to be formed during the Pliocene and that climatic change occured during the Quaternary, a rational approach

to the analysis of the present-day distribution of the fauna is to consider the history of the landscape in relation to climate and organisms.

2.5.1 The Haffer-Vanzolini Model

It is generally accepted that the origin of the present day fauna of the Neotropical region is Tertiary. As a corollary, several students assumed a long-term evolution, a gradual transformation of organisms to create the present day diversity of animals (and plants). The working hypotheses have been a slow change in the landscape, change with some direction, "trends", change which created more and more empty niches and new lineages to fill them. As one of many examples, I quote the following: "The climatic conditions at that time Early Pleistocene have been such as to support large forests but, since the Pleistocene these climatic conditions may have changed from humid to the present drier conditions, which support the dominant, savana, floral climax... My idea is that a tropical forest still covered the Central Plateau of Brazil in (early?) Pleistocene times and that Proechimys of a primittive type... lived in that extensive forest-climax. As a result, a large cliseral change was initiated, which shifted the forest-climax to the more humid eastern escarpments and lowlands... while the savanna climax was being established on the plateau...An arid belt was developed which now constitutes an efficient geographic barrier to the distribution of many kinds of animals." (Moojen, 1948).

The assumption in the above passage is that evolution is always a slow process, that landscape also changes slowly, and that long-term trends in evolution are the most relevant ones. This

leads to the idea that phyletic graudalism is the chief evolutive path. Dispersal centres are viewed as entities which exist during long periods in stability. These ideas have been the dominat ones in zoological thinking (e.g. Muller, 1973; Patterson & Pascual, 1972; Hershkovitz, 1962). The Central Plateau in Brazil has been seen as the primary dispersal centre for South American Mammals by almost every authority in the last fifty years (e.g. Hershkovitz, 1962, 1963, 1968, 1972, 1977). The Amazonian forest is rich because it is old, is another conclusion based on th se assumptions. Recently, a critique of these points of view has been developed and an alternative model for speciation in South America in the Quaternary has been proposed. This is the Haffer-Vanzolini model.

The Model

It is assumed that climatic fluctuations conditioned two sets of vegetational cover over South America: the first occuring during the humid phase: when the forest formations were the most important cover for the area north of parallel 30°; the second set occuring during drier conditions and consisting of wide-spread open formations with the forest reduced to patches (fig. 2.9). The alternation of dry and wet periods created a situation in which during the dry periods, the population of organisms related to forests became isolated, "refuged" in the forest patches. When the climate turned to wet again, the forests grew up throughout areas previously occupied by open formations, coalescing the refuge areas. Formerly isolated populations cama again into contact. When these populations meet again, genetic divergence resulting from isolation is reflected in the

in the taxonomic structure: some forms are given specific status, some can be described best as sub-species and others have very complex patterns of differentiation. The argument about refuges is that in the Amazonia, they are peripheral to the region and determined by topographical features. A convergence of edaphic hydric and dynamic climatic factors is responsible for the location of the refuges. The peripherality of the refuges in Amazonia and the speed of climatic change is responsible for the wealth of forms in this area. When the refuges come in contact differentiated populations mix and form the basis for an even greater diversity during the next refraction (Haffer, 1969; Mayr, 1969; Vanzolini, 1970, 1973; Vanzolini & Williams, 1970).

A basic tenet of the model is that geographic speciation (Mayr, 1942, 1963) is the major speciation process. The result of the constant and speedy advance and retreat of the forests. is the richness of species observed in the Neotropical forests.

The use of the model

Several students of South American biology have been using the same basic idea. Haffer (1967, 1969, 1974) used it to explain speciation in birds; Prance (1973) for certain groups of plants; Brown (1975) for Heliconiini butterflies; and Spaasky et. al. (1971), for two groups of Drosophila. The study of these various taxa led to the designation of several possible refuge areas which were reviewed by Brown (1975) who summarized the present knowledge (Fig. 2.11). When it is intended to analyse the geography and systematics of any Neotropical taxon today, the model must be used. The model has, however, some limitations, as Vanzolini (1970) pointed out: some taxa will be distributed in

Figure 2.11 - Quaternary Forest Refuges in South America

1 - Darien
2 - Nechi
3 - Choco
4 - Chimboraz
5 - Cauca
6 - Magdalena
7 - Catatumbo
8 - Rancho Grande
9 - Sucre/Trinidad
10 - Apure
11 - Villavicencio
12 - Putumayo
13 - Abitagua
14 - Napo
15 - Maranon
16 - Huallaga
17 - Ucayali
18 - Chancamayo
19 - Inambari
20 - Yungas
21 - Guapore
22 - Imataca
23 - Roraima
24 - Parima
25 - Imeri
26 - Manaus/Guiana
27 - Oyapock
28 - Belem
29 - Tapajos
30 - Rondonia
31 - Madeira
32 - Tefe
33 - Loreto
34 - Araguaia
35 - Bahia (Ilheus)
36 - Rio de Janeiro
37 - Missiones

(Based on Brown, 1975 and Ab'Saberm, 1977b)

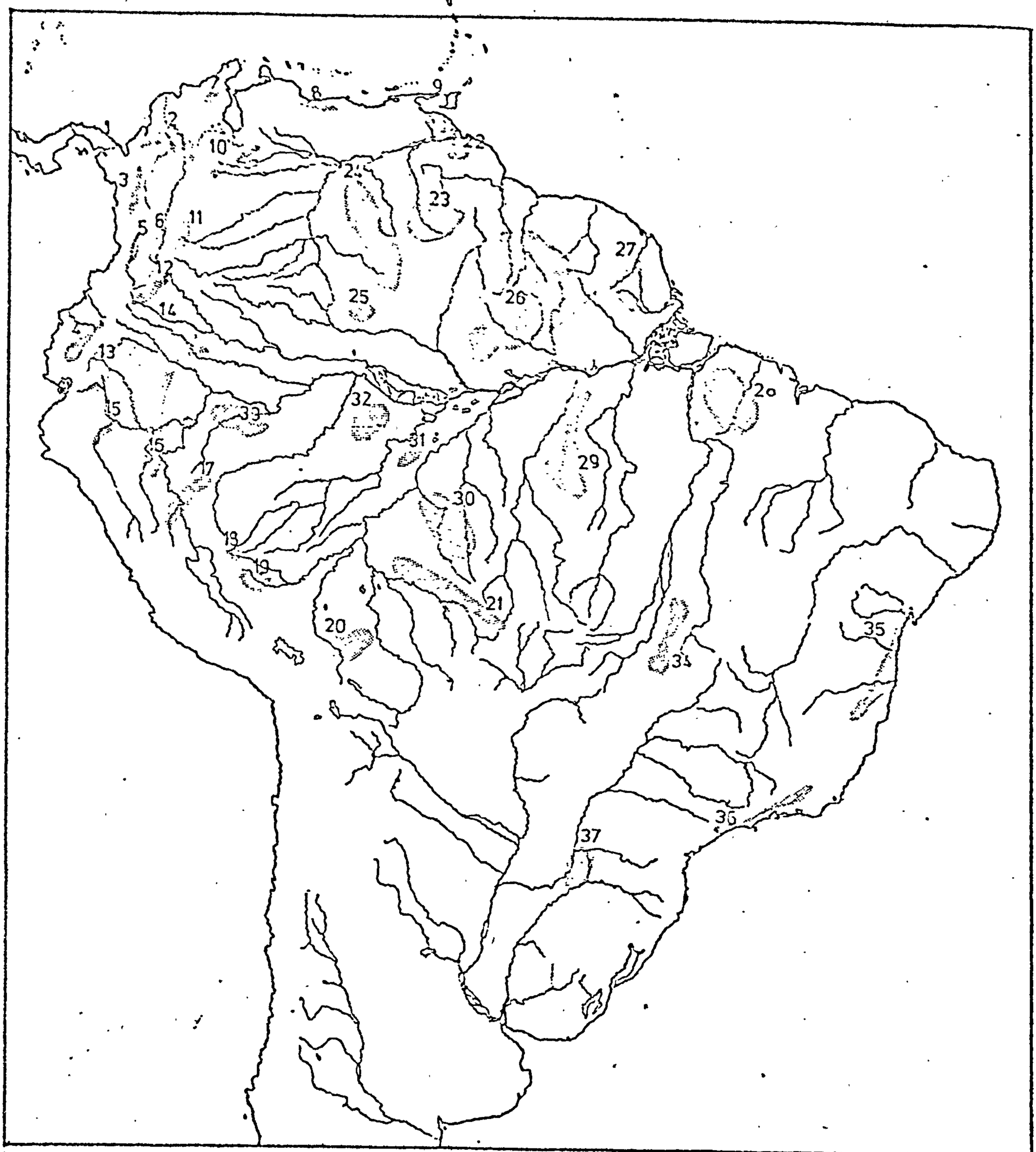


Figure 2.11 - South America's Quaternary Forest Refuges

in relation to environmental facttrs, others will have a special distribution related to certain habitats inside the domains (Cerqueira, 1976; Vanzolini, 1970), etc. But the model is useful even in some of these cases (Cerqueira, in preparation).

When one taxon shows sister groups occuring in disjunct areas or when it has parapatric distribution inside a forest domain without an apparent barrier, the first step to take is to see if these groups may be related to past climatic events. Generally speaking, sub-species, semi-species or closely-related species in South American forests belonging to a group of species were usually related to refuge areas which existed during the upper Pleistocene/ Holocene.

Disjunct sister groups could perhaps be found in forests which today have no connections. Within the same domain, parapatric distribution is more common.

The higher the taxonomic level of the sister group, the greter the probability that differentiation occured in the Pleistocene. As will be discussed, some groups which are today restricted in distribution, can also be related to refuges in the past.

In the next sections some taxa of mammals and some general implications of the model will be discussed.

2.6 SPECIATION AND EVOLUTION OF NEOTROPICAL MAMMALS

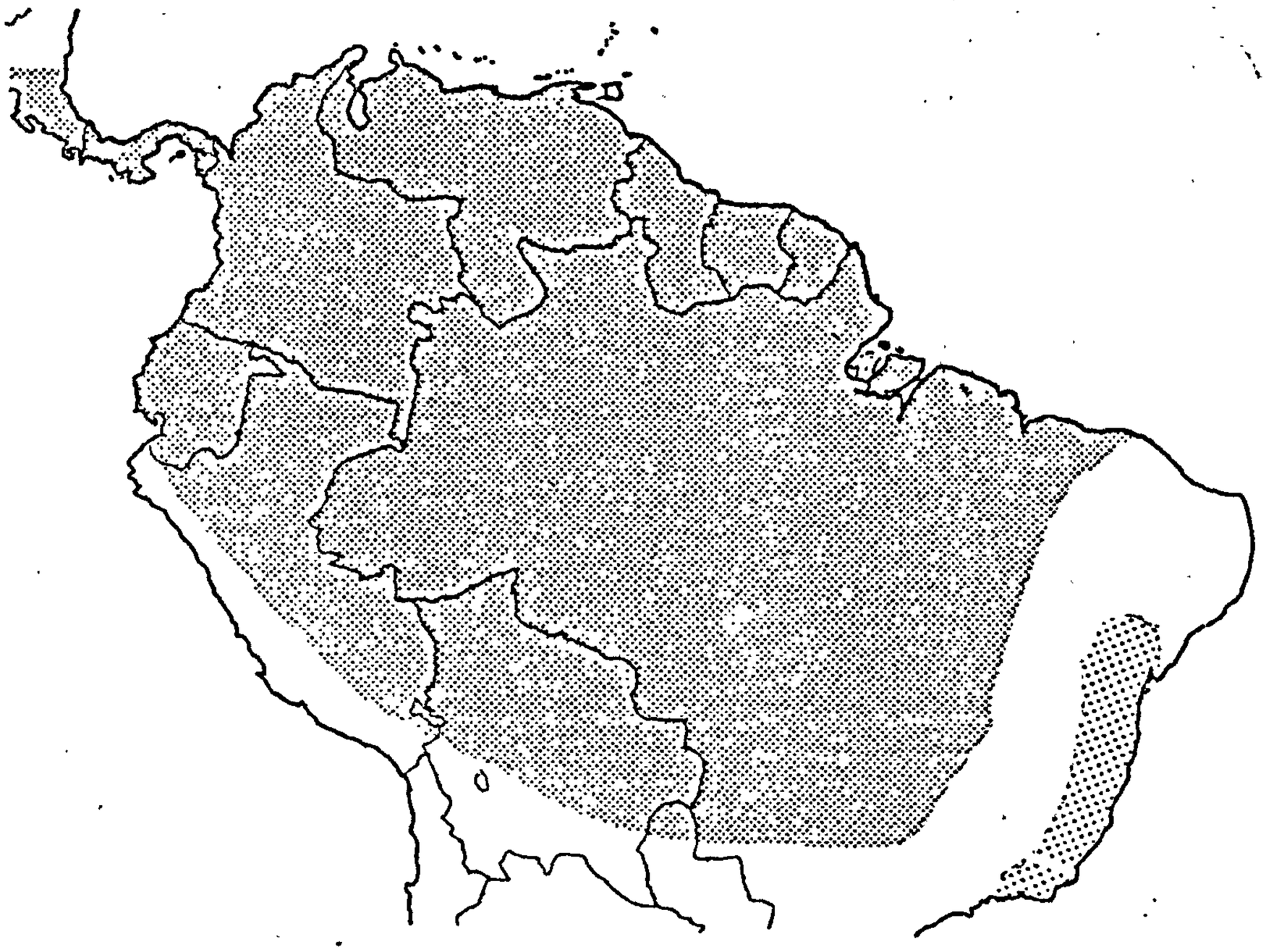
The knowledge of South American Mammals is still very fragmented. For some groups, such as the Primates, we know with some accuracy, the number of species and their boundaries, and have at least a rough idea about their variation. Recent research has indicated that some taxa are more difficult to understand than

was previously thought. Primate systematics are based chiefly on coat colour while for some other mammals, this character is almost useless. However, due chiefly to the lifelong work of Phillip Hershkovitz on Neotropical Mammalogy, some taxa can be used as a basis for general evolutionary studies.

Some cases which seem to be suitable for analysis have been selected for discussion below.

2.6.1 Rodents

Proechimys - This genus was reviewed by Moojen (1948) who considered the genus as constituting two sub-genera: Proechimys and Trinomys. The former inhabits the forests of northern South America and Middle America, and the latter the forest of eastern Brazil (Fig. 2.12). Moojen listed eight species, seven with a total of twenty-nine sub-species. Hershkovitz (1948) considered three more species bringing the total number of species to eleven, with thirty-three sub-species. Cabrera (1961) made a somewhat different arrangement of the genus, considering twelve species and fifty-five sub-species. None of these arrangements can be considered definitive. Walker (1975) says that twenty species appear to exist. It is nevertheless evident that the two sister groups inside the genus (i.e. the sub-genera Proechimys and Trinomys) could have been a product of a split between the two major forest regions (i.e. the Hyleae and the Atlantic Forest). Inside this forest speciation occurs. It is also clear, at least in the Atlantic Forest, that the steeped variation among the forms in this domain is linked with the refuges considered for the area: Moojen (1948) considered three species in the forest and one in the transitional belt between the forest and the Cerrado and Caatinga. One forest



Subgenus Proechimys

Subgenus Trinomys

Figure 2.12 - Distribution of the Genus Proechimys (Rodentia,Echimidae) (After Moojen,1948)

species is in the Reconcavo Bahiano, probably linked with the Ilheus refuge, another in Rio de Janeiro. Moojen (personal communication) told me that the latter region, visited by him, is very wet, similar to the Hyleae Bahiana.

An interesting feature of Proechimys distribution is their absence in the southern part of the Atlantic Domain.

I suggest that the split between the two sub-genera occured before the last glacial, since within Trinomys speciation and subspeciation have occured. To account for this, it seems necessary to consider two other climatic episodes splitting the forest, one responsible for the division which led to speciation and the other for the formation of subspecies. Since chromosomal rearrangements seem important in Proechimys evolution, it is possible to postulate that [illegible]sipatric speciation occured. The data at hand however indicate that even if this sort of speciation is to be found, climatic change and fluctuation are important as well.

To test this hypothesis it is necessary to re-evaluate the present sistematics of the genus with the refuge theory as a framework. Cytogenetic and biochemical studies are other methods indicated to establish a new classification. However, the present picture is enough to support the link between refuges and speciation in the genus.

Oecomys - This genus comprises at least two groups of species (Figs. 2.13; 2.14). Both groups are chiefly amazonian. Hershkovitz (1960) considered Oecomys, (a subgenus of Oryzomys) as being composed of two species: Oryzomys (Oecomys) concolor and O. bicolor. Karyological studies carried out by Gardner & Patton (1976) demons-

Figure 2.13 - Distribution of the group Oecomys bicolor (adapted from Hershkovitz, 1960). The letters refer to Hershkovitz' subspecies, numbers refer respectively to n number and FN number in Chromosomes.

Figure 2.14 - Distribution of the group Oecomys concolor (adapted from Hershkovitz, 1960). Letters and numbers as in Fig. 2.13.

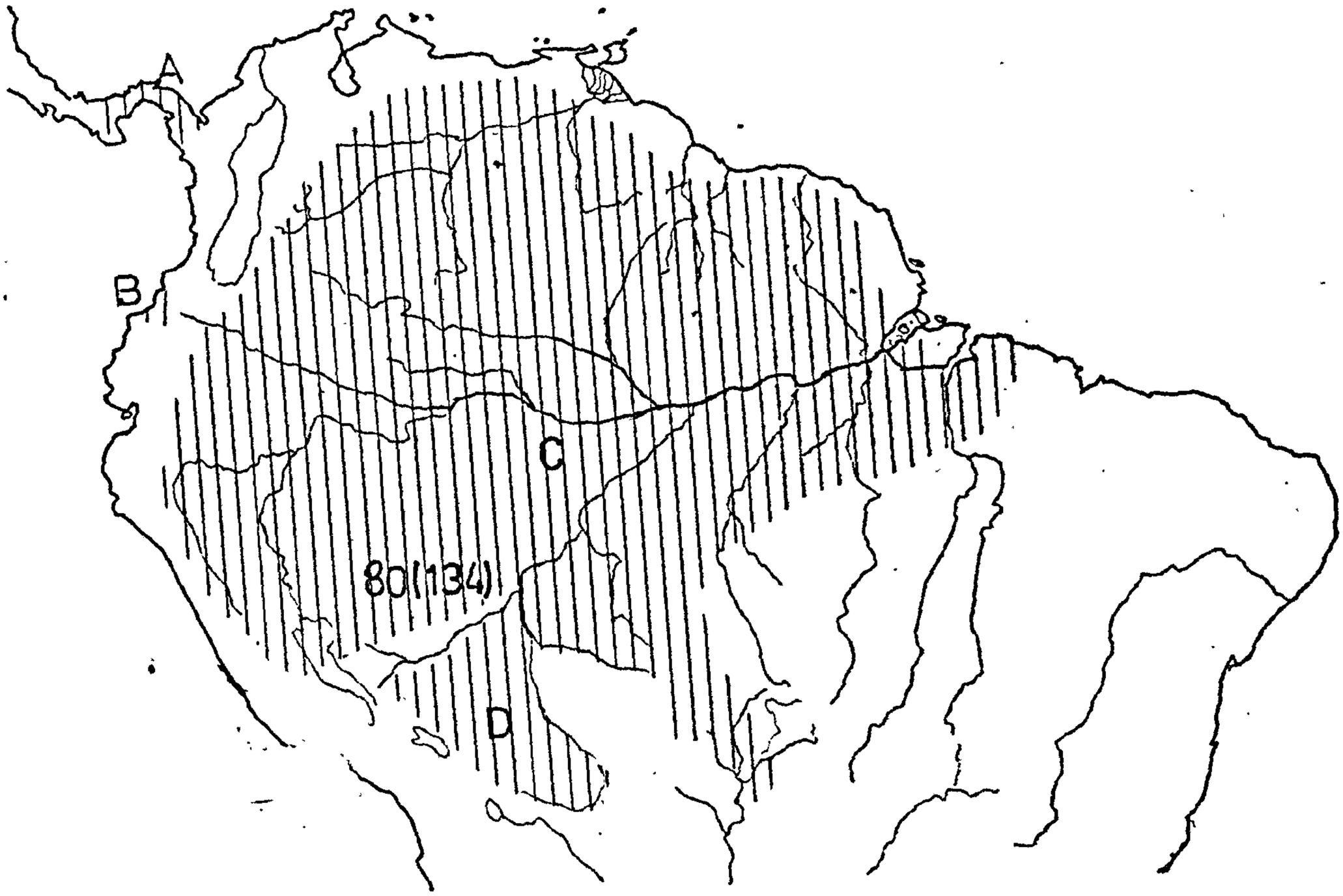


Figure 2.13

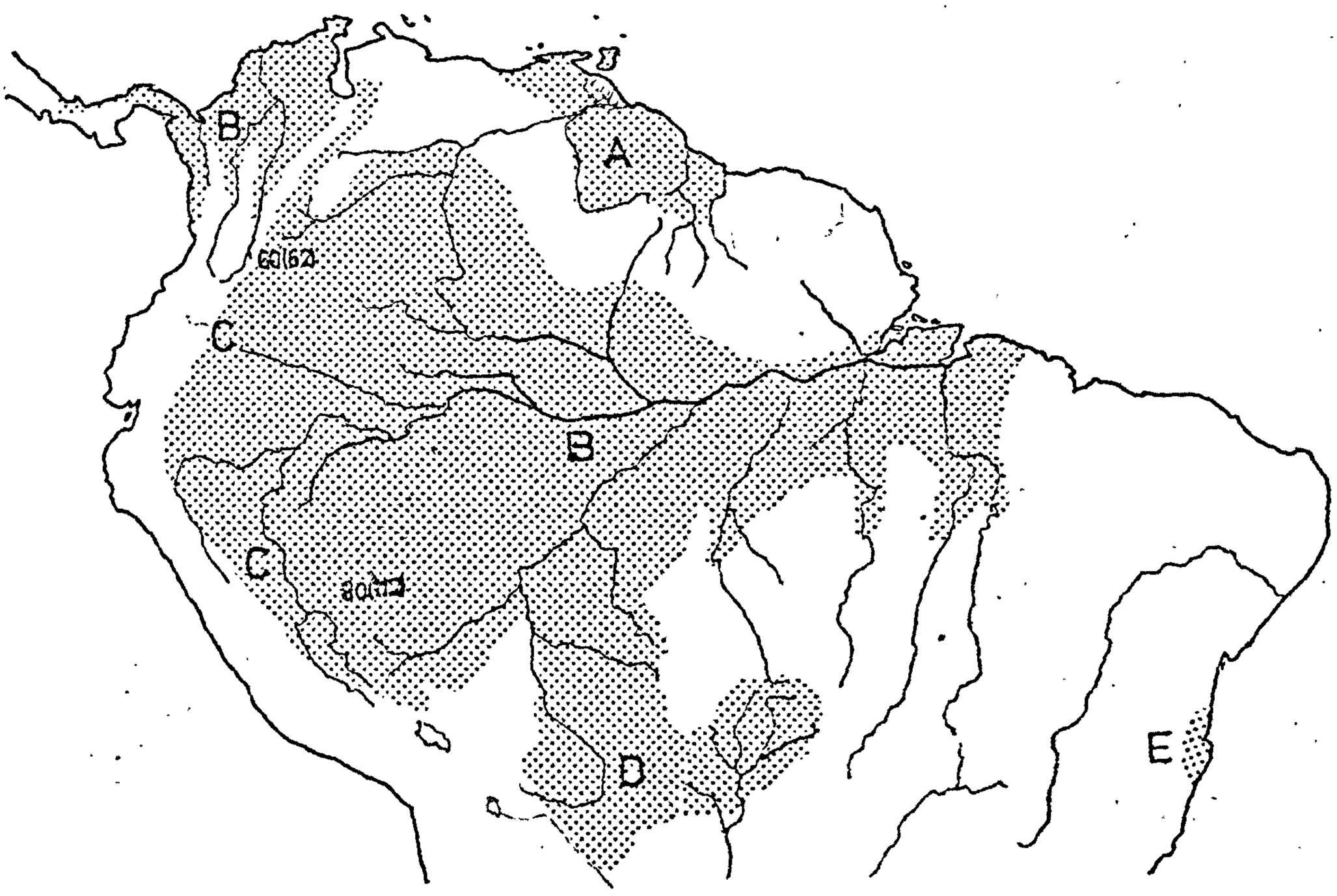


Figure 2.14

trated that the first species is a composite, as could be seen from samples from two localities of namely concolor types, one 2n = 80, FN = 112 (one specimen examined in Loreto, Peru) and the other, 2n = 60, FN = 62 (8 specimen from Villavicencio, Colombia). Specimens from only one locality of bicolor were examined by them as well.

The new data is difficult to consider in relation to the pattern of variation presented by Hershkovitz (1960). As for most Cricetid Rodents, it is at present almost impossible to know how may species exist in each genus of this family.

However, the distribution of both groups of species is interesting. The bicolor group apparently has a disjunct distribution. A set of forms exist in the Amazonia and in the foothills of the Andes. Two other forms are transandean, one occuring in the region of the Choco refuge (Fig. 2.11), the other in the region of the Darien refuge approximately. The disjunction seems to be recent since the morphological differences between these sets are not very large (Hershkovitz, 1960).

The concolor group also has a disjunct distribution one from occuring in the Ilheus region, in the Tropical Atlantic Domain, the other in Amazonia and other rainforests in northern South America and Middle America. The disjunction shown by this genus can be explained in terms of a formerly continuous distribution being split during subsequent arid periods. The concolor group could re-invade the re-forested areas in the North but the population in Bahia remained isolated and endemic in its "amazonian" refuge on the Atlantic.

The genus Oecomys itself, judging from available cytogenetic data, differentiated in the Amazonia and its origin, as well

Figure 2.15 - Distribution of Rhipidomys (Rodentia, Cricetidae) in Eastern Brazil. Data from samples in the Museu Nacional, Rio de Janeiro. Two groups of forms are recognized: 1 - "R.mastacalis", localities A,B,1,2,3,4,5,5a, and 9. 2 - Unamed form, localities C and 8. Localities 6 and 7 may belong to the second group. Letters, type-localities; numbers, other localities.

A - Serra do Ibiapaba, (Type-locality of R.cearanus Thomas)

B - Lagoa Santa, Minas Gerais (Type-locality of R. mastacalis (Lund)

C - Parati, Rio de Janeiro (Type-locality of an yet undescribed form)

1 - Sao Benedito, Ceara

2 - Ipu, Ceara

3 - Caruaru, Pernambuco

4 - Garanhuns, Pernambuco

5 - Barreiras, Bahia

5a- Bom Jesus, Bahia

6 - Feira de Santana, Bahia

7 - Jequie, Bahia

8 - Ilheus, Bahia

9 - Terezopolis, Rio de Janeiro

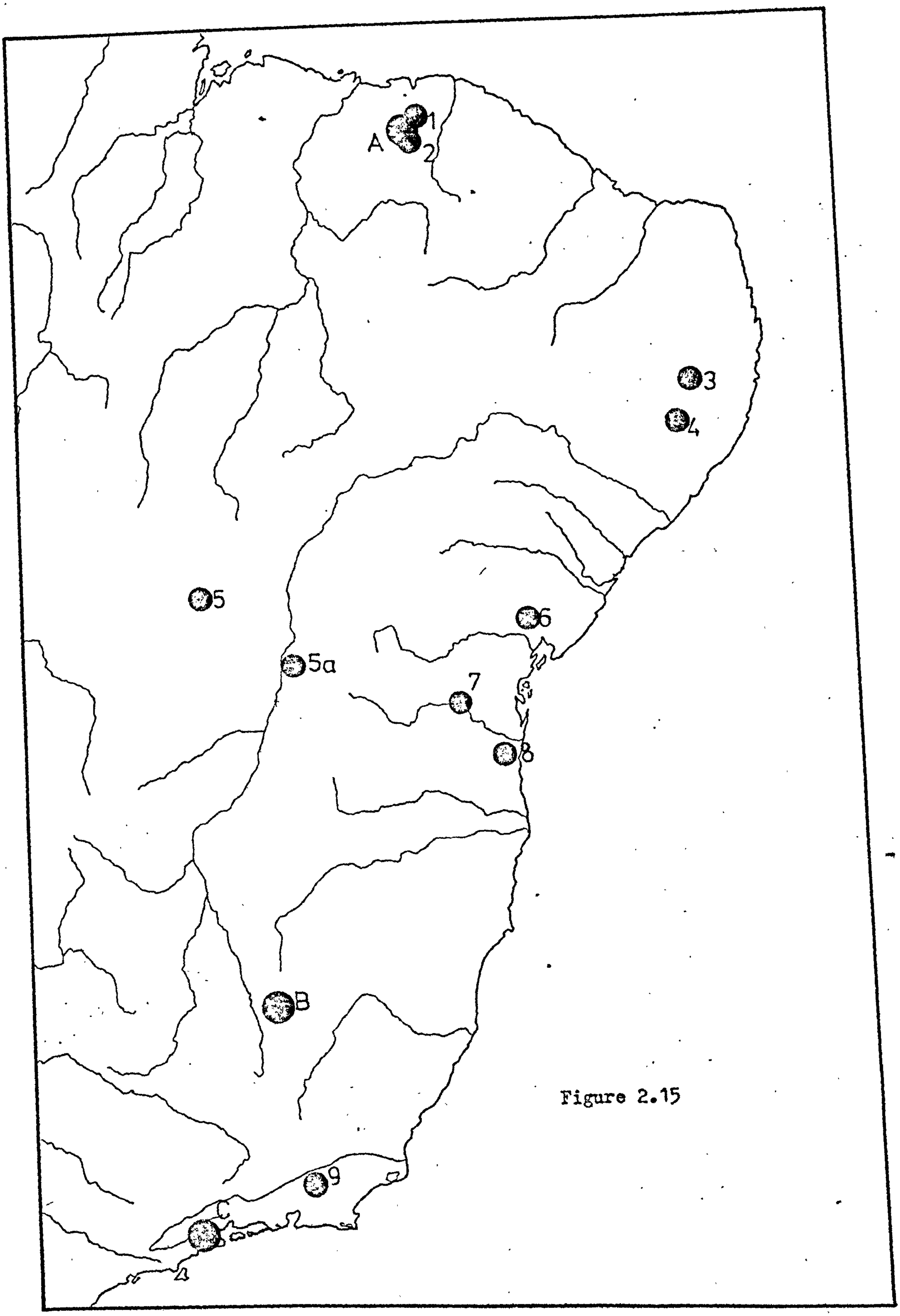


Figure 2.15

as the origin of its species, was probably linked iwth the same kind of change in the environment.

Rhipidomys - The genus occupies a large area in South America, but I am concerned here with the forms which occur in Eatern Brazil. There is no revision of this genus and the last comprehensive arrangement was by Cabrera (1961).

These rodents are adapted to arboreal life, being in general forest dwellers. I have examined several specimens from some localities of Eastern Brazil (Fig. 2.15). In Cabrera's arrangement (1961), all of them belong to the nominal form "Rhipidomys mastacalis", however the specimens from some localities 1, 2, 3, 4, 5, 5a, 9, A and B form a set of populations which can be assigned tentatively to this form. The sample from Ilheus is similar to the one from Parati. Both samples amy be subspecies of a species which is undboutedly different from "R. mastacalis". Even within "R. mastacalis", as considered above, I doubt if all are conspecific. The cursory examination I have made suggests that the forms from the Northeast (localities A, 1, 2, 3, 4) set a natural group. Samples from Bahia (excepting Ilheus and maybe Jequie and Feira de Santana) belong to another group and Terezopolis is probably within the range of the form of Lagoa Santa.

The degree of differentiation gives a clear picture: The samples C and 8 are linked with moist forests. Probably they belong to a group which exists in all the Atlantic forests. Its internal differetiation is due to isolation in the Serra do Mar and Ilheus refuge (Fig 2.11). The Terezopolis (9) sample is interesting because even in the Atlantic forest it is apparently the same form as is found in Lagoa Santa in the Cerrado. Lagoa Santa

is on the border of this domain and Rhipidomys seems to be able to occupy gallery forests and "Cerradoes" (Woodland savanas). Probably in the last very dry episode, Rhipidomys mastacalis, invaded the Serra do Mar and remained there. The form, yet unamed, of Parati and Ilheus apparently is more restricted in its requirements and does not occupy dry forests. Differentiation in the "R. mastacalis" group may have occured in the Atlantic forest north of Bahia. This forest is almost separated from its southern counterpart in the domain by the decidious forest belt which surrounds the Atlantic forest in the Northeast.

It is not yet completely understood how the pattern exemplified by this genus appeared. Maybe the differentiation between the two major groups occured before the last glacial, and during this period the present day pattern took shape. It is possible as well that the split of this group occured in the last major dry period, when the Atlantic forest was split into refugia. "R. mastacalis" then occupied its present range through gallery forest, differentiation being accelerated by Holocenic climatic fluctuations.

Thomasomys - This genus is said to be typically "andean". It is part of a group of closely related genera, the Thomasomyine group (Hershkovitz, 1966). All described forms are andean, inhabiting the forests in the temperate, subtropical slopes (Hershkovitz, 1969, 1972; Walker, 1975). However, a group of forms related to Thomasomys occur in eastern Brazil, belonging to the namely genus Delomys. I accept here provisionally this genus as a separate entity. Another Thomasomys, T. oenax, occurs in Southern Brazil and Uruguay.

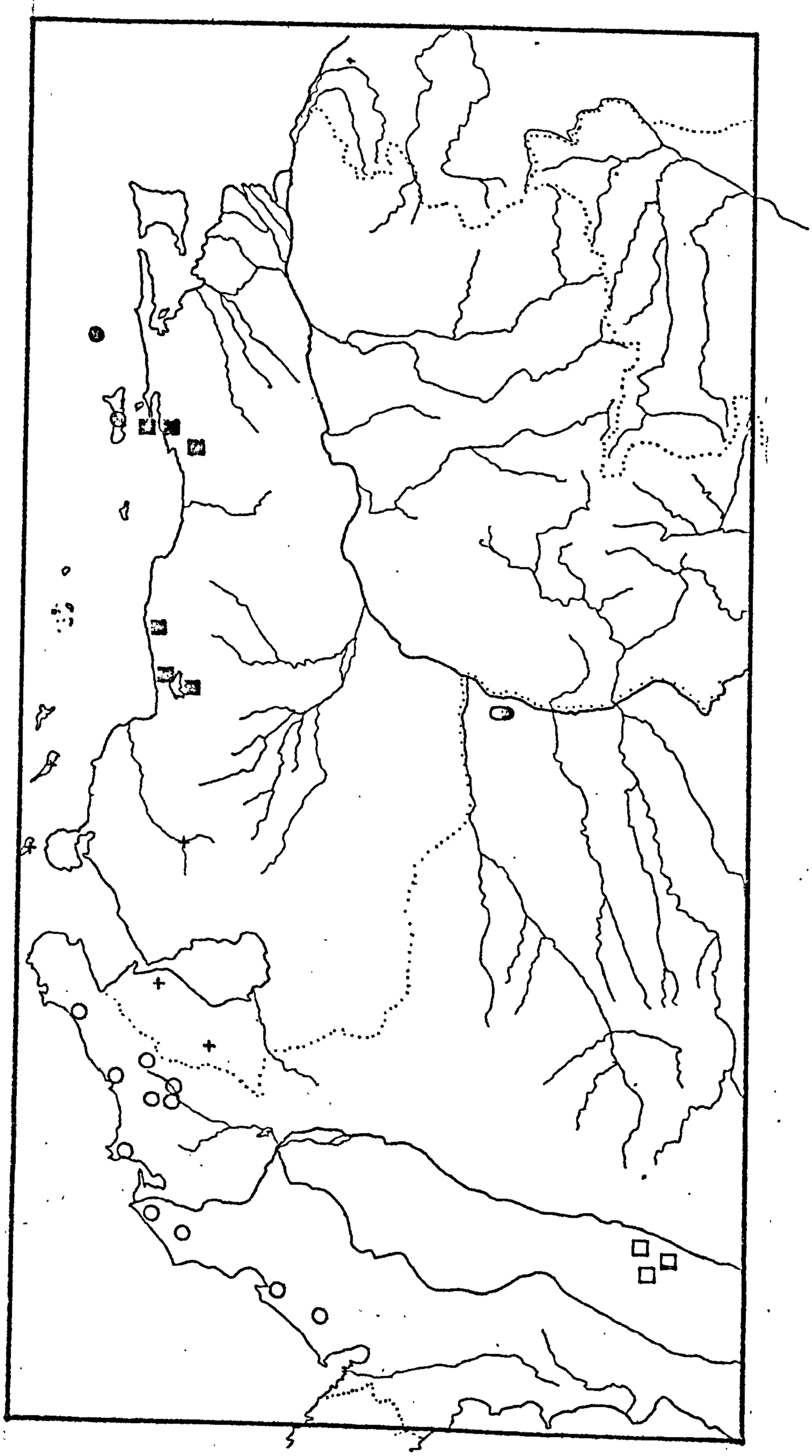
Analysisng the distribution of Thomasomys, Rhipidomys, Phaenomys and Delomys, it can be seen that only Rhipidomys has a widespread distribution (Cabrera, 1961) and the other limited in their range. The following hypothesis can be made to account for this distribution. Thomasomys as a stem group, could have invaded lowland forests in early Pleistocene and subsequently, differentiated into the other genera. The differentiation of these genera probably was an early phenomenon with Phaenomys becoming isolated in a refuge in the Serra do Mar while Thomasomys (or a pre-Thomasomys group) remained refuged at the Andean foothill. Later, "Thomasomys" re-invaded the lowlands and the following retraction of forests isolated Delomys and Rhipidomys. Reinvasion of some areas made these genera sympatric in parts of their ranges. Character displacement may have occured to allow this sympatry. Little is known about the Ecology of these forms. Rhipidomys is arboreal (Hershkovitz, 1969, 1972). Thomasomys may be terrestrial-scansorial, but T. oenax is arboreal. T. lugens is said to nest in trees but has typical terrestrial small eyes (Walker, 1975). Phaenomys is a very specialized form, red rust coloured, which seems characteristic of some terrestrial forms of animals in rainforest. It can be postulated that the group evolved from terrestrial to arboreal or vice versa. If the first postulate is correct, the Phaenomys differentiated earlier than Rhipidomys and Delomys. As a relic it points to this hypothesis. I think the whole of Thomasomini group can be understood by understanding the advance and retraction of forests. Inside each genus a thoughtfull analysis will reveal the same principle operating again, as demonstrated by Rhipidomys (q.v.).

T. oenax is not the zoogeographical problem some zoologists have claimed it to be. It is actually a relic of the former extension of the present equatorial andean vegetation in the upper Pleistocene. Changes in the environment of its present day range may be is the cause of the rarity of the species, which like Phaenomys, could scarcely survive the changing environment, while Rhipidomys succeeded in doing so.

2.6.2 Silvilagus - Two speices of this genus occur in South America : Silvilagus floridanus and S. brasilienses. This latter form has at least 21 named subspecies. S. Floridanus inhabits a semi-arid tropical region of Colombia and Venezuela. Seven subspecies as recognized by Cabrera (1971) have the distribution shown in fig. 2.16. Without discussing the validity of the present taxonomic arrangement, it is noteworthy that the patterns shown by this species is linked with the present day distribution of semiarid regions. This species seems to be competitively excluded form the forested areas by S. brasilienses (Hershkovitz, 1950). The present distribution is difficult to explain by any dispersal mechanism. It therefore seems more likely that the present distribution was caused by the splitting of a former area which, during a drier past episode, comprised the present ones where the cottontail rabbit is found. Since S. floridanus ranges from the United States through Middle America to Colombia and Venezuela with differentiation only at the subspecific level, the invasion of South America by these rabbits probably occured in the Upper Pleistocene, in the last dry period of the Pleniglacial. Subsequent high humidity phases divided the range of the species in South America during the Holocene causing its present pattern

Figure 2.16 - The Cottontail Rabitt in Northern South America.
Silvilagus floridanus' Classification by Cabrera (1961, distribution by Hershkovitz (1950)

- ● S.f. avius
- + S.f. continentis
- ▣ S.f. cumanicus
- ⌀ S. f. margaritae
- □ S.f. purgatus
- ⌀ S.f. orinoci
- O S. f. superciliaris



of differentiation.

2.6.3 Tamandua - According to Wetzel (1975), two species of this Edentate occur in the Neotropics: Tamadua mexicana and T. tetradactyla. The two species shows character displacement in several characters but apparently there is no simpatry, one species displacing another in their ranges.

Large sample studies by Wetzel (op.cit), in relation to coat colour, led him to conclude that "...melanistic tamandua are, perhaps, examples of the saturate stage before progressive subtraction of melanin to paler, more uniformly colored individuals as discussed by Hershkovitz. This may have been triggered by cross mating between population formerly isolated in late Pleistocene along the Andean foothills and the Guyana highlands with those from the highlands of Brazil (see Vanzolini, 1973)." Wetzel considers the use of the refuge model as having the best explanatory value since it accounts better for the evidence of clinal variation in several characters.

2.6.4 Tapirus - According to Hershkovitz (1954) three species of these Periosdactyla exist today in the Neotropical Region. Hershkovitz believes (op.cit) that each species appeared in North America and then invaded the Neotropics. However Haffer (1970) pointed out that there is a distinct possibility: only one immigrant gave rise to the three forms, Tapirus pinchaque, the Andean form, occupied the rising Andes during the Pliocene/Pleistocene, T. terrestris occupied the lowlands east of the Andes and, maybe T. bairdi, differentiated from the latter in the Choco Refuge

during one dry episode.

Excepting the Andean form of tapir, the distribution of this genus is somewhat similar tothe Caviamorph Hydrochaerus, the Capybara, if H. isthmius is considered a distinct species. H. hydrochaerus occupies partially the same range as T. terrestris and H. isthmius occupies partially the same range as T. bairdii (Mones MS). Both genera seem to occupy similar habitats in the region but their adaptive zones are quite distinctive. The similarities in the distribution of both taxa point to Neotropical differentiation of Tapirus, since Hydrochaerus is typically a Neotropical group.

2.6.5 Primates

Modern knowledge of Neotropical Primates began with Hill's revision (1957, 1960, 1962). The present good state of knowledge of this taxon is due chiefly to the work of Philip Hershkovitz. He recently published the first volume of his encyclopedic review of New World monkeys. Here I shall use some examples taken from his work which I think can supply evidence of relevance to Pleistocenic chance in mammals speciation.

Family Callithrichidae - Without discussing its validity, I accept here the phylogenetic relationships among Callithrichid genera as established by Hershkovitz (1977). These relationships are roughly summarized in fig.2.17 . In fig 2.18 the present range of the family and its constituent genera is shown. Two genera (Cebuella and Saguinus) are "amazonian" and two others (Callithrix and Leontopithecus) are "atlantic". All of them are forest dwellers but Callithrix also inhabits Savanas and, probably, some types of woodland Caatinga.

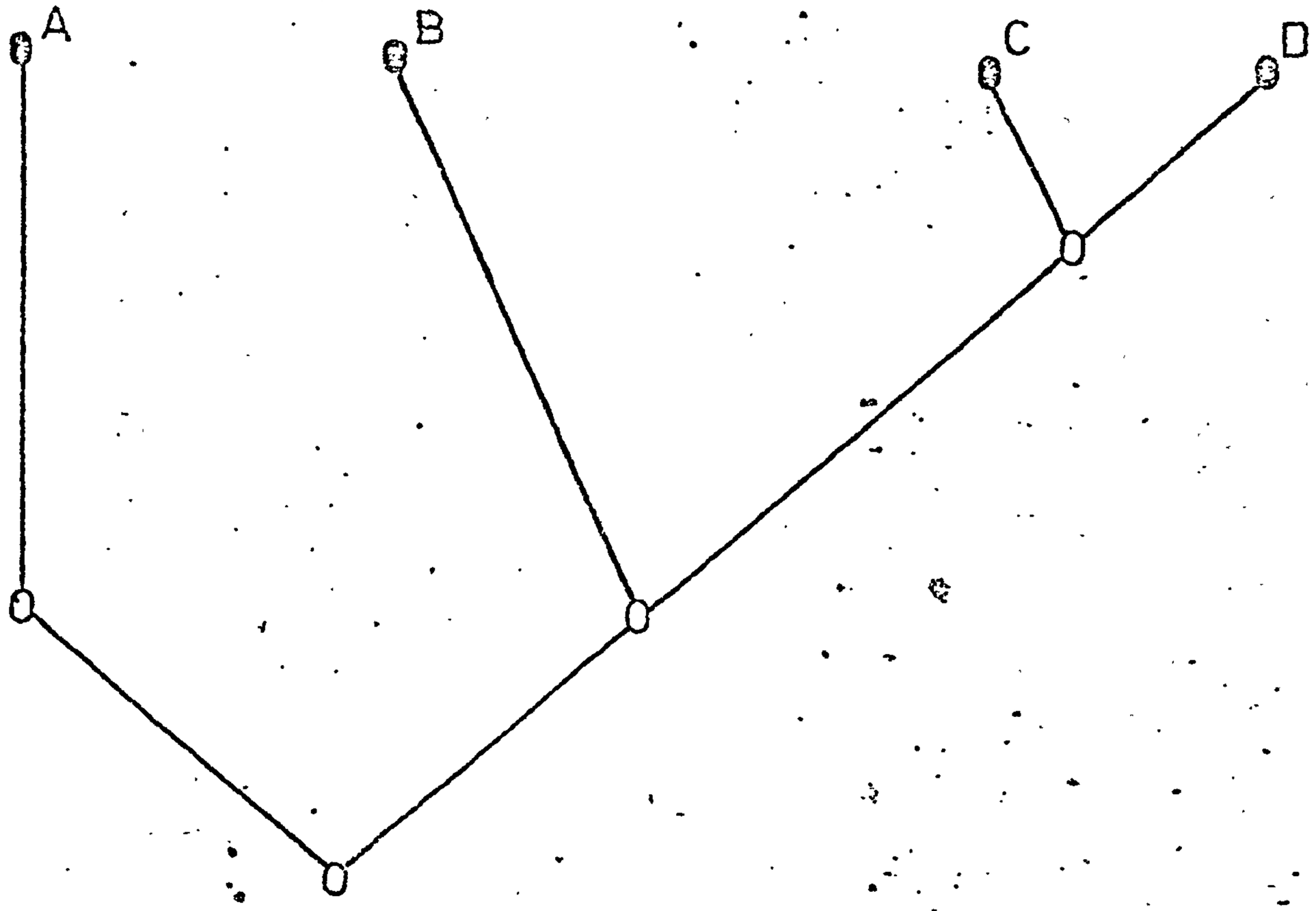


Figure 2.17 - Possible relationships among Callitrichid genera. Based on Hershkovitz (1977). Internal relationships in the genus Callithrix not shown.

A - Cebuella

B - Leontopithecus

C - Callithrix

D - Saguinus

Hershkovitz interprets the distribution and phylogeny of this taxon as an "ancestral form" occuring in the "Brazilian Highlands centre of origin", and afterward:emigrating to Amazonia and the Atlantic Forests where the present genera differentiated. However, I suggest an alternative hypothesis: the ancestor of the family occured continuously in late Pliocene or early Pleistocene in the area ranging from the Atlantic coast to the Amazonia through part of what is today the Cerrado area. Climatic change expanded the Cerrados isolating populations in the foothills of the Andes, the Serra do Mar and, maybe, in "Brejos" refuges. The fact that the area occupied by Cebuella houses several other forms of Mammals endemic to the region is probably due to the persistence of forested areas in the region through the Pleistocenic climatic vicissitudes. After the first punctuation in the ancestral lineage, two groups emerged: the pre-Cebuella and the pre-Leontopithecus. Reoccupation of the whole range was achieved again by one or both groups. A second change led to a second punctuation when Leontopithecus (or a direct ancestor) arose. Pre-Callithrix must have emerged at this time. Callithrix shows ability to range in drier conditions than the other genera. I suppose that either the Callithrix evolved in some Atlantic refuge or in the "Brejos" and at the same time Saguinus arose in the Andean foothill refuges, or that Callithrix differentiated in some Amazon basin refuge while Leontopithecus did so in the Atlantic forest region. Since the most "primitive" group of Callithrix is the jacchus group, an eastern Brazilian taxon, I prefer the first hypothesis. the following changes in the landscape account for the specific and subspecific differentiation within these genera.

Figure 2.18 - Distribution of the Family Callitrichidae showing the ranges of its extant genera (Based on Hershkovitz,1977)

Figure 2.19 - Hypothetical reconstruction of events leading to the formation of modern Callithrichidae genera.

1. A - Ancestral form

2. A - Cebuella or pre-Cebuella

   B - pre-Leontopithecus/Callithrix

3. A - Cebuella

   B - pre-Leontopithecus/Callithrix

4. A - Cebuella

   B - pre- Callithrix (?)

   C - pre-Saguinus (?)

   D - Leontopithecus (?)

5. A - Cebuella

   B - pre-Saguinus (?) or pre-Callithrix (?)

   C - pre-Callithrix (?)

   D - Leontopithecus

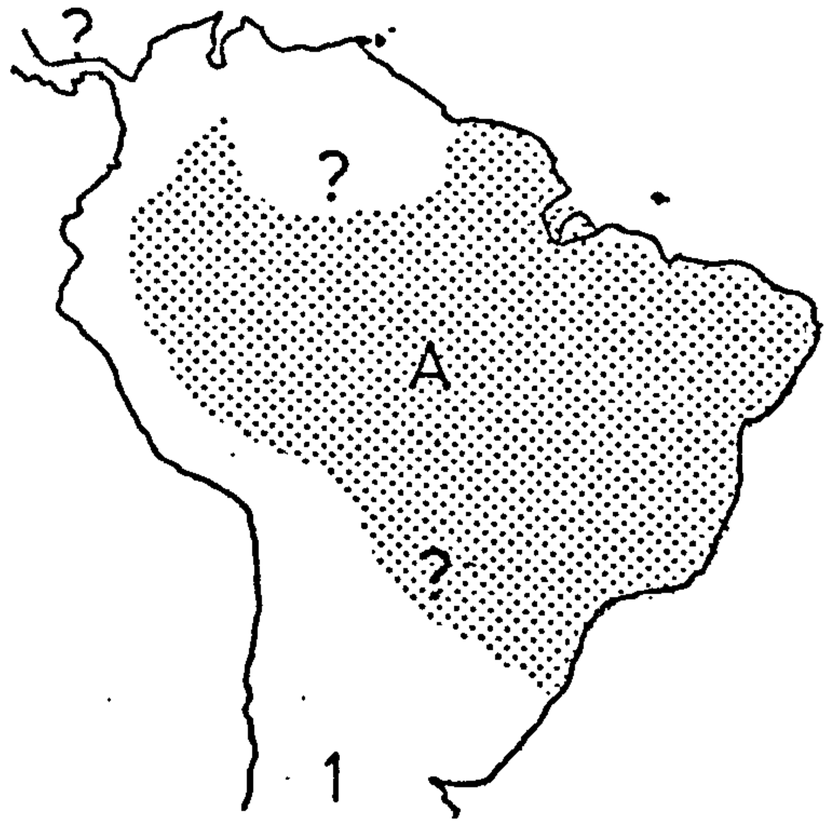
6. A - Cebuella

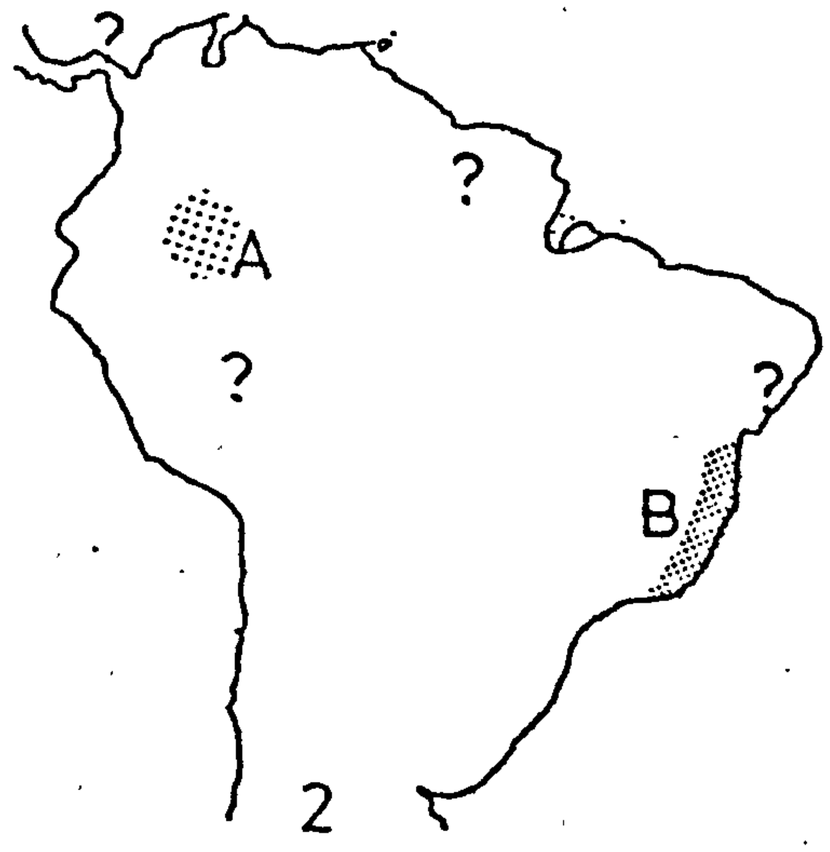
   B - Saguinus

   C - Callithrix

   D - Leontopithecus

The ranges are only approximate, no attempt to precision was made. Events 1,3,5 corresponding roughly to wet (pluvials?) phases, 2, 4,6 to dry ones. More explanation in the text.





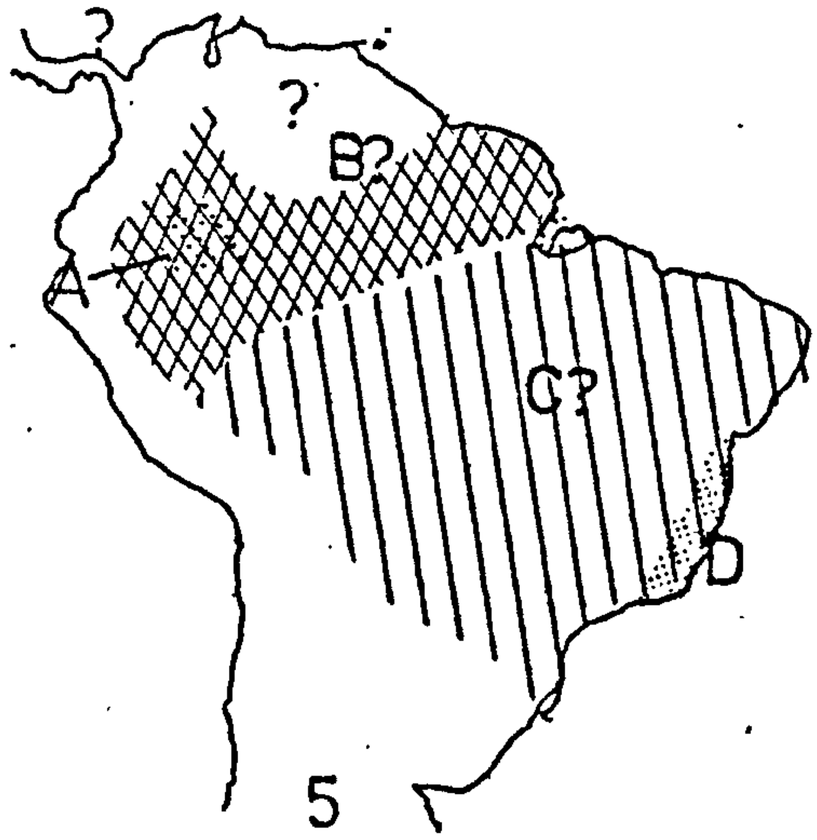


Figure 2.19

As Cebuella remained restricted in area, in a more stable region (in forest terms) its rate of evolution was lower, accounting for its present "primitiveness". Occupation of its territory by the related Saguinus could have occured because the differentiation of Saguinus is a late event, Saguinus occupying a quite distinct adaptive zone (Moynihan, 1970; Hershkovitz, 1977). Callithrix and Saguinus seem to exclude each other in their respective zones. The first occurs in areas which are very diverse ecologically, and interms of area size it is the most succesful of all Callithrichids. Figure 2.19 summarises the above discusion. Other comments on some of these Primates are made below.

Cebuella - Restriction of Cebuella to its present range (fig. 2.17) can only be explained in historical terms, since it is difficult to see any obstacle to its occupying the whole of the Amazonia. It is possible that Cebuella existed in other areas of the domains in the past, but it became extinct when the forest was reduced. Since the large refuges are near its present range, one can suppose that an area effect combined with random events led to its present restriction. I suppose that sister groups normally are to be found in Amazonia. As several species occur in the same region as Cebuella the absence of sister groups can be explained by the persistence of the refuges in the foothill of the Andes through the toughest dry phases of the Plestocene.

Leontopithecus - Leontopithecus rosalia, the sole species of the genus is divided into three well-marked races (Fig. 2.18 and fig 2.21). White settlement after the XVIth century divided the Tropical Atlantic Domain forests and the remnants of the Lion Marmoset are

are today restricted to some small pathces of forests in the States of Bahia, Rio de Janeiro and Sao Paulo (Coimbra-Filho, 1969; 1970; Coimbra-Filho & Mittermeier, 1973a). In historic times, the species ranged from Bahia through Espirito Santo and Rio de Janeiro to Sao Paulo (Fig. 2.~~20~~21). Hershkovitz (1977) considers that the differentiation of modern forms was due to the contraction of forests in a dry episode of the Pleistocene. Even today, the two northern forms Leontopithecus rosalia chrysomelas and Leontopithecus rosalia rosalia range approximately in the areas which formally were the Ilheus and Serra do Mar Pleistocenic refuges (cf. fig. 2.11). I doubt whether the third form Leontopithecus rosalia ~~chrysomelas~~ chrysopygus is related to the Missiones refuge (2.11). If this assumption is true it can be assumed that either this form had been differentiated later than the other two by geographical variation, or another refuge area exicted in Sao Paulo. In either case, the subspeciation of Leontopithecus rosalia is a late event which probably occured in the last glacial.

Cebuella - This genus is restricted to the Western end of the Amazonia. Other forms such as, for instance, Callimico(fig. 2.21) Philander mcilhenny (Gardner & Patton, 1972), Lagothrix (Fodden, 1963) inhabit the same area (of course the ranges are not identical). The chief core area of the region is the refuge. I shall discuss later the significance of the regularities in the distribution of mammals in the region.

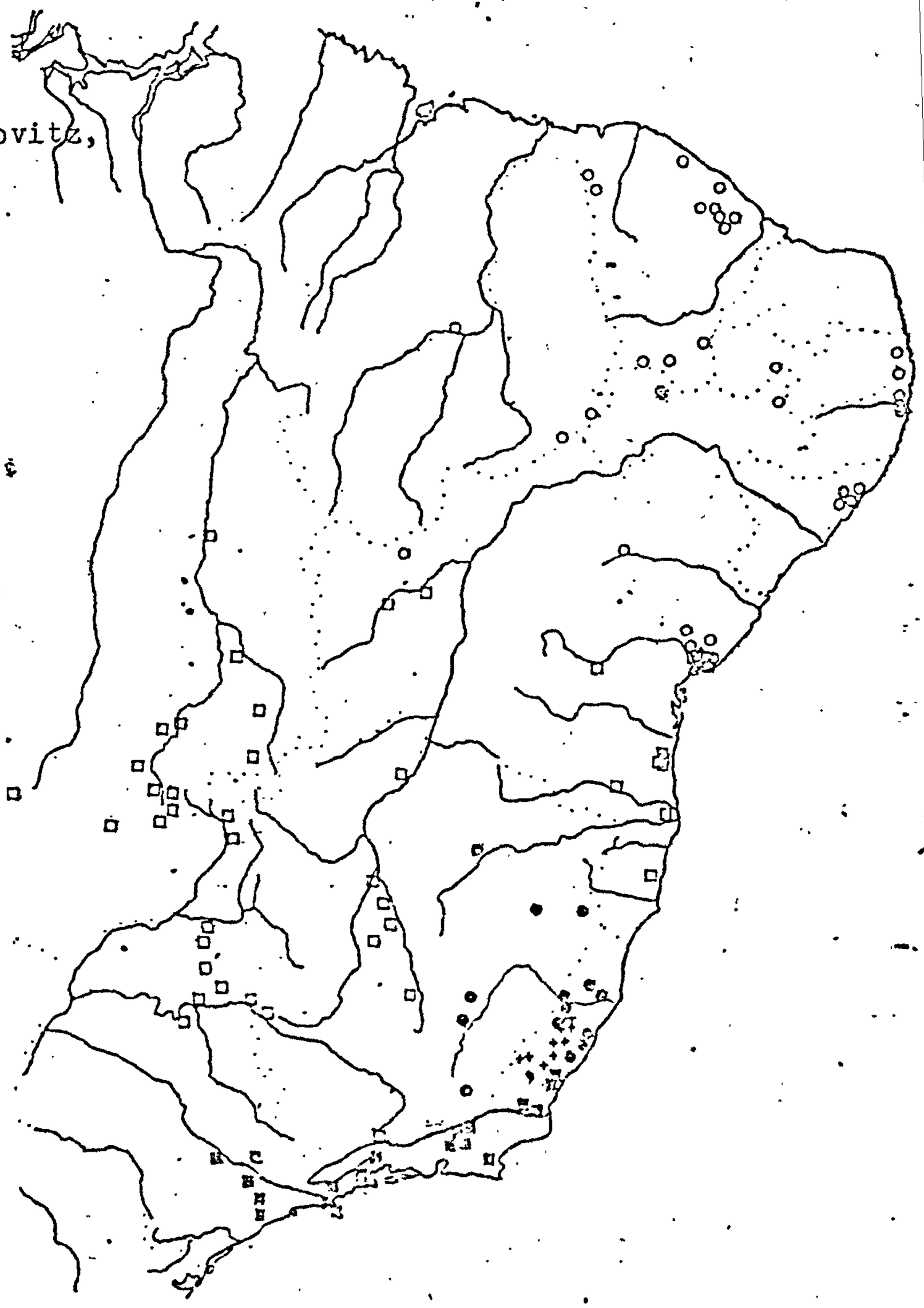
Callithrix jacchus - This species inhabits a large area in eastern Brazil. Hershkovitz (1975, 1977) recognizes five subsepcific forms (Fig. 2.20). Two of them inhabit rainforest regions (C. Jacchus

aurita, C. j. flaviceps). Three others exist both in rainforest and dry, semideciduous ones (C.j. geoffroy, C. j. penicillata and C.j. jacchus). The pattern of distribution observed is somewhat usual for the region. Some odd features are presented by Hershkovitz. He says that all subspecies are sharply defined and that rivers and climate are barriers for the subspecies. But it is difficult to understand why the Rio Sao Francisco is a barrier for C.j. jacchus in the upper stream but not in the lower stream. At the same time, the same form inhabits rainforests, caatingas and cerrados but, apparently cannot live in the same kinds of open formation south of the Rio Sao Francisco. The other forms present similar features. At the same time he states that "If Callithrix jacchus originated in Brazilian highlands" and "from this center C. jacchus radiated east into the humid coast and northeast into the arid Northeast Region." If "C. jacchus" had a center of origin and radiated, why are its forms sharply defined, showing no clinal variation between them but only intergrades when and where two forms met? On the other hand, judging from his review, at least C. j. jacchus has clinal variation in its range. These evidences presented by Hershkovitz himself, are contradictory to his interpretation of the origin and evolution of this group.

Coimbra Filho & Mittermeier (1973a) reviewed a series of papers by the senior author, who has been conducting a research program on hybridazation among marmosets, and concluded that "C. jacchus" is a group of closely related species. However, as almost all forms have hybridized in captivity and Hershkovitz has presented (1975) some possible cases of natural intergrade, it seems that these forms

Figure 2.20
Superspecies Callithrix jacchus. Based on Hershkovitz, 1977.

- ○ C.j.jacchus
- □ C.j.pennicillata
- ● C.j.geoffroy
- ■ C.j. aurita
- \+ C.j. flaviceps



are semispecies in a superspecies, lineages which have attained some degree of identity but are not yet "good" species. There is no theoretical problem in this assumption (See Simpson, 1961; Wiley 1978).

Apparently, the forms of this kreise were originated by the split of the environment of an ancestral species. They show interesting cases where some complications occured on the contraction of the forests during a dry period. C.j.flaviceps* is restricted to the eastern slopes of Serra do Caparao, State of Espirito Santo, and has not been recorded from the western slopes. The region is (or was, in the past) forested. Little is known about the region. This serra is part of the Serra da Mantiqueira. In this region these mountains are high and steep, contrasting with other parts of the Serra da Mantiqueira in the hinterland. Ab'Saber (1977b) considers the possibility of a refuge in this region. Analysing the climatic factors of the region (i.e. pluviosity, termal range, average temperature, insolation, evaporation, cloudiness, relative humidity and effective rainfall (index of Thorntwaite, given by BRASIL, MINISTERIO DA AGRICULTURA,(1969)), it can be suggested that this area could have been a refuge. On the other hand, these populations of marmosets appear to be restricted by altitude (Hershkovitz, 1977 and references in that book). C.j. aurita, one of its neighbouring forms, may be related to another refuge, the Serra do Mar one (fig 2.11)

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*I am avoiding here the use of different names from those used by Hershkovitz. Anyway, the degree of differentiation is so low that in fact these forms are in an intermediate situation between species and subspecies, even if I prefer to call them "species" the reality is a superspecies, that is, a complex of forms. At the same time, this is not a correct place to discuss nomenclature, according to the international code.

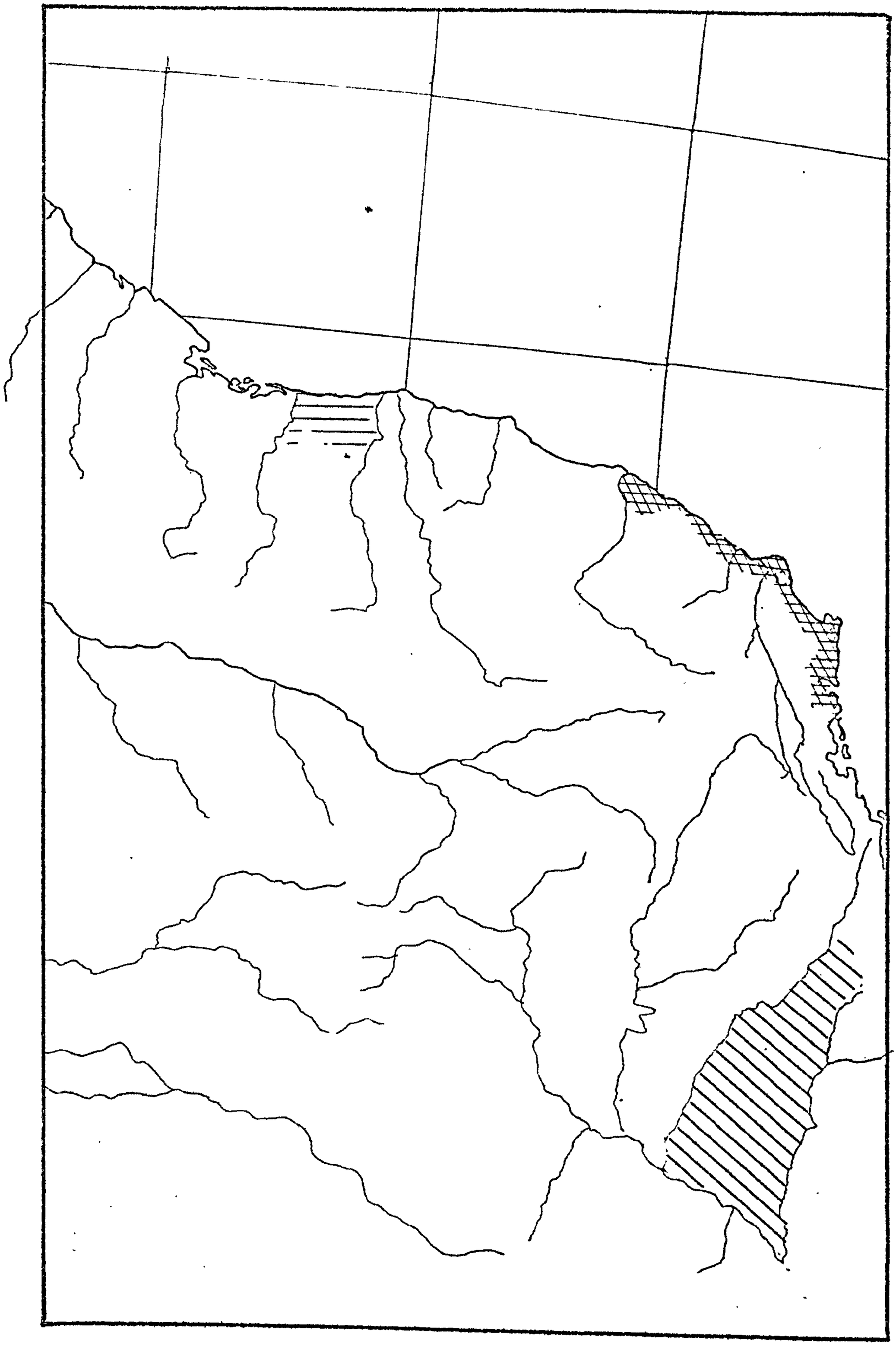
The other neighbour C.j. geoffroy inhabits the narrow lowland strip between the Serra do Caparao and the sea, and also the Rio Doce valley and the Serra da Mantiqueira west of Caparao. Taking into account its present distribution, no refuge can be related to this form.

About the remaining two forms, C.j. jacchus and C.j. penicillata it can be said that the former may have originated from coastal forests and the latter in the Ilheus refuge.

As was discussed above, forests probably occupied larger areas before the last glacial maxima. Even if in the Northeast the semi-arid character remained (Ab'Saber, 1971), the evidence points to the existence of links among the present day "brejos" (refugia). In the Cerrado higher rainfall probably altered some parts of this biome, favouring the Cerradao (Woodland savana, in some ways a kind of forest) and some lateral expansion of the gallery forests. Subsequent dry period restricted populations of C. jacchus to (from North to South): 1. a very narrow strip of forest in the Northeast; 2. the Ilheus refuge; 3. the Serra do Caparao and 4. the Serra do Mar refuge. Around the areas 1 and 2, gradation of aridity allowed the persistence of dry forests. Populations of C. jacchus may have persisted scattered through them.

At the same time, the coastal lowlands were enlarged by marine regression and the Restinga vegetation occupied a larger area. This vegetation is derived chiefly from the Atlantic forest. The high salinity in this environment causes physiological aridity even if, as today, the water content of the environment is high. Of course a larger coastal plain with Restinga was not so affected by the sea, but the aridity of these times had the same effect as salinity on it. However, coppices and larger patches of woodlands are part of restinga landscape and C. jacchus probably occured

Figure 2.21 - Distribution of Leontopithecus rosalia in Eastern Brazil. Based on Coimbra Filho & Mittermeier, 1977.



in that area. The picture that may be construed is: pre-aurita and pre-flaviceps went to the refuges. The latter developed a link with altitude. Parapatric evolution (Endler, 1977) occured in a way that it allowed pre-geofroy's existence in the Restinga and dry lowland forests of Rio Doce Valley.

Increasing humidity changing th distribution of vegetation allowed the expansion of these populations.

Other Primates - In Herskovitz' book, other examples of the working of this general mechanism of Neotropical evolution can be found. The Callithrix argentata group has a pattern clearly linked with refugia in the Amazon valley and in the foothills of Andes. The same applies to the Saguinus nigricollis group. I believe that, as a whole, the Callithricid history is linked to climatic fluctuations and forest refugia.

Similar conclusions can be drawn from the genera Ateles (Kellog & Goldman, 1944), Callicebus (Hershkovitz, 1963), Cebus (Hershkovitz, 1949c), Lagothrix (Fooden, 1963), Saimiri (Cabrera, 1957), all of them belonging to the family Cebidae.

2.6.6 Cave Fossil Mammals of Eastern Brazil

In Lagoa Santa, Minas Gerais, several limestone caves bear bones of fossil mammals. Paula Couto (1975) reviewed these fossils and attributed 96% of the genera to the Lujanian (Upper Pleistocene). Recent excavations have been made in the region. The material obtained is being studied by Dr. Fausto L.S.Cunha and his team in the Museu Nacional, Rio de Janeiro, and he told me thht all absolute datating so far has indicated an Upper Plestocene/

Holocene range of age for the deposits. The majority of the fossils from this region was collected and studied by Lund in the last century and he probably mixed fossils, subfossils and mammals from owl's pelets. However, some extinct and extant mammals are noteworthy.

Myocastor coypus was found in the caves. Presently its distribution is restricted to colder areas in the South. Several ungulates occur as well: Notoungulates, Litopterna, Perissodactyla (Hippidion and Equus) and Artiodactyla (Palaelama, a large fauna). All of these forms disappeared. Two species of bear, genus Arctodus occured as well. This genus is closely related to the Andean Spectacled bear, Tremarctus.

These fossils give evidence of cold climate in the past. The presence of "andean" forms, together with "southern" ones points to support the idea of a link between the Araucaria forest and the Andean forests. The nature of these links is not clear, but it is assumed that the Araucaria forest may have extended to the region. Some kind of intermediate vegetation in the area of the present Araucaria and Andean forest probably occured but its features can only be guessed. The evidence supports the idea of both the permanence of the Cerrados in some areas of the Brazilian highlands and of the larger extension of the South American forests in the Upper Pleistocene. In addition, the distinction between fossil and extant animals, at least the generic level, shows that different complex of vegetation existed. The last glacial maximum and its arid conditions changed the whole picture (Fig 2.9), extinguishing several mammals of this fauna.

2.7 INTERIM DISCUSSION

To finalise this chapter some points related to its subject must be discussed. Other theoretical considerations will be made later.

The landscape (i.e. the physical and biological factors in the earth surface seen as a whole) has an effect upon its constituent organisms. Its change poses the need to change for the animal and plant as well. In South America it is now known that wholesale climatic change affected this continent as it did the others. However, the data are scattered and insufficient. Thus, even a periodization is difficult. There is a general tendency to formalise events, to consider that the phenomena are generally clear-cut. This is not the actual case for geography or biology. The climatic change is rapid but the curve leading to the maximum cold is not the gentle roundness of the model. Actually, the story is one of fluctuations, minor advances and retreats of ice sheets, of rainfall increasing and decreasing, etc. At the same time, forests, forest refuges, meadows, savanas, etc., changed continuously their ranges, even their internal structures, with all effects of a changing environment being felt by its inhabitants.

The history of mammals of South America is therefore one of animals submitted to a constant change of the very place where they live.

I tried to picture the complex interplay between mammals and the landscape. However, to assemble data was difficult. Even the as well-catalogued mammals, as the Primates, have been studied in a formalistic framework. Evidence for clinal variation, for instance,

usually is not given. Therefore I have to use as data the classification of a group as being a species or subspecies. Since species are actual entitites, even when their internal variation is not well-known, the study of their internal structure, i.e. infra-specific variation, shows certain regularities in geographical terms. This is a reason to use the approach I used. Some points must be made about the implications of these regularities. Although they will appear again later, they are discussed in the following sections.

2.7.1 Tertiary and Quaternary as Different Periods

A very simplified picture of the Tertiary landscape was presented. Lillegraven (1972) pointed out that a major change in the number of mammalian taxa occured in the Oligocene and in the Quaternary. I have not examined the data concerning the Tertiary with detail to discuss the Oligocenic events. From the Pliocene onwards, the evidence suggests that the change was greater than in any other Cenozoic period, since not only were some major physical features of the landscape changed, but the composition of the Neotropical biota was profoundly transformed as well.

These facts lead one to consider that the Pleistocene must be analysed as a separate geological epoch. Therefore, the present day fauna is something which has an historical explanation in the Pleistocene. Familial and suprafamilial taxa may have histories longer than the range of the Quaternary, but I am not concerned with them here.

2.7.2 Refuges

The map of refuge areas (fig. 2.11) is a tentative formal-

ization of a rather complicated phenomenon. It is useful for the naturalists as a reference picture, but it must be understood as a formal representation of a process.

The "brejos" of Northeast Brazil can be seen as a model for these refuges. These "brejos" are sometimes very clear-cut regions where the environmental conditions are very different from the surrounding ones. The destruction of forests for agriculture gives other examples. Barrett (1979) showed that some mammals inhabit only the coppices of secondary growth forests in the belt between the Atlantic forest and the Caatinga. Others can live both in the cultivated or abandoned fields as well as in the coppices. When a field is abandoned, forests can grow somewhat faster. The compositinn of the pionner vegetation is different from the nearby forest; some species, however, are later an important part of the forest biomass (Sasanna Hecht, personal communication). Surrounding the rainforest dry deciduous or semi-deciduous forests may occur. Again, for some animals, dry forests are an extension of their rainforest habitats. The third kind of extension of a forest is the gallery forest. I think I could include narrow strips of forest which exist along the slopes and bottoms of ravines in a similar category as in the Gran Sabana (Vila et al., 1965) and those which are seen in Tabuleiro dos Martins, near Maceio, Alagoas, which is a low altitude plateau, covered by Cerrado-like vegetation.

All of these rainforest extensions can function as enlarge ments of the refuges area for some species.

The tropical rainforest is very diversified, with a large number of species, large total biomass but with the biomass of each species being generally low in relation to the total biomass.

It can be imagined, if some species can exist in dryer conditions than the rainforest ones, that these species will be even more abundant around the refuge. It can be assumed that for some species the harshness of the environment found outside the rainforest is compensated by a lessening of the competition and by the relatively greater abundance of particular plant species. The same assumptions can be applied to the gallery forests. In the first case, the transition to open areas is almost sharp. In the second, the forest can extend through the banks from one forest to another. All these features can be seen today. For instance, between the Amazon forest and the Cerrado, a deciduous dry forest occurs. Actually, the transition in general is rainforest, deciduous dry forest, "cerradao" (Woodland savana) cerrado (Ab'Saber, 1971,1977; Askew, et. al. 1971; Ratter, 1971; Rizzini & Heringer, 1962). A gallery forest shows a change in constitution along the course of a river. A gallery forest which begins in a given forest starts with a species composition similar to the main forest. However, this composition changes progressively through its course (Cabrera, 1953). The adaptability of a given species determines the extent to which it can live outside the refuge. Some species could probably live in the whole of the Amazonia, since they could occupy all available space through the gallery forest. Differentiation in these cases is probably due to distance and also to the weakening of gene flow (since one can expect that the populations in a small area has a more hazardous existence). Other species could occupy only the surroundings of the refuge, while some others were restricted to the rainforest.

Since the ecological valence varies from one species to another, almost every species had a unique spatial distribution

The core of the superimposed tracks of all species corresponds to the core of the refuge. The packing, with subseq ent reduction of the resource spaces (MacArthur & Wilson, 1967), was related to the area of the core, but a large number of species did not suffer because they managed to inhabit areas outside the core area.

The distributional pattern of some forms can be explained in a similar way. Animals which could inhabit the deciduous dry forest were adapted to an environment which is a transitional form between forest and open areas. Therefore, during a humid period the possibl extension of dry woodlands caused the extension of the range of such species. They managed to occupy the cerradao, and sometimes, the woodland caatinga, from the dry forest belt around the rainforest. This phenomenon probably explains the distribution of Rhipidomys, Proechimys, and Callithrix in Eastern Brazil. I suggested elsewhere (Cerqueira, MS) that the transition from forest to open area habitats by Cricetids Rodents can be explained in the same way.

In the Western Amazonia (fig. 2.11) more refuges have been postulated than in any other region. I think that the forests of the Equatorial Andean Domains were never disrupted in the region. Hence the available area for some taxa was quite large, since the Andean forests are almost continuous with the rainforests. The packing of species in such area did not lead to a substantial shrinking of the habitat occupied by each species. Several taxa are restricted to this region. These taxa probably had a former large range but the effects of area shrinking extinguished them elsewhere

In general the refuges can be roughly compared with islands but the equilibria in them are different since their species are not"immigrants", they existed there before, but when the forest shrink the number of available habitats decreases.

Origin and extinction of species - Vanzolini (1970, 1973) pointed out that the abundance of forms in the South American rainforest, is due to the expansion and contraction of forests. The other side of the coin of speciation is extinction. Both can be explained in terms of the Red Queen hypothesis of Van Vallen (1973): The faster the rate of environmental change, the faster the Red Queen must run to stay in the same place. Climatic and environmental change was rapid in the Pleistocene and some species were not able to adapt quickly enough. Wholesale extinction may be due to an acceleration of environmental change.

The area effect discussed above is just one important aspect of this change."Community evolution" occured at a fast pace. The general mechanism could have occured before, with more or less intensity (Lillegraven, 1972; Van Valen, & Sloan, 1977). The Red Queen running in"normal" periods causes the observed constant rates of extinction of each taxon (Van Valen, 1973) but in these revolutionary times the rates can be accelerated.

2.7.3 Vicariance and marginal populations

Croizant, Nelson & Rosen (1974) have criticized the idea of Centres of Origin, chiefly in the extremist Matthusian form. I have demonstrated that the origin of most of the Neotropical Mammal fauna can be better explained in a vicariance model. It must be noted that the refuges are not center of origin, but regions where vicariant populations get isolated. I cannot see any good evidence supporting the widespread idea of the Brazilian Highlands as the chief centre of origin of most South American mammals. Hoojen (1948) was correct when he adopted a vicariance model for

the genus Procchimys (however, using a gradualistic point of view). Unfortunately, the dispersal model was used and refined more and more in all subsequent work on the subject. I agree with Varzolini in seeing the South America fauna as Pleistocenic, its species bein mostly Upper Pleistocene/Holocene in origin. The whole picture of landscape/biota history sets the conditions where fast rate of evolution is possible. This again, explains the extinction and origins of mamal groups in the Quaternary. It explains as well, the rate of evolution of Cric tids rodents which has been seen as being so fast thatthey "must" have immigrated earlier than the Pliocene (Hershkovitz, 1972). However, the fossil record is probably the correct picture: Cric tids invaded South America in the Pliocene, occupied part of the available resource space and were submitted to the climatic change. They differentiated and exploited their adaptative zone and survived. Other animals which could not do the same became extinct.

CHAPTER III

ECOLOGY OF DIDELPHIS

INTRODUCTION

The ecology of South American Marsupials is not well known. Only the Virginia opossum, Didelphis virginiana, has been extensively studied and most of the generalizations about this genus, as well as other Didelphis, have been based on this species.

In the course of the present research, I have examined a large number of specimens collected in 289 localities all over South America, plus some Middle and North American ones. The data obtained from the study of the geography of these localities enabled me to study the factors affecting the distribution of the opossums. Data obtained in the Museu Nacional, Rio de Janeiro about the places of collecting and about some characteristics of the animal trapped, were used as well. This information is presented here. I shall discuss the reproduction first, and then go on to discuss some aspects of the ecology.

PART A

REPRODUCTION

3.A.1 Introduction

Two groups of opossums exist in South America, the Didelphis marsupialis the black-eared opossum, and the Didelphis albiventris, the white-eared opossums. I could gather some new data for the analysis of reproduction of D. albiventris in North-eastern Brazil. When necessary, reference is made to other species which have been studied. Some comparative statements are also made.

Most of the material used was collected during the course of a research project on plague endemics. This project was conducted

by the former Servico Nacional de Peste (SNP, National Plague Service, Brazilian Ministry of Health). The collecting of mammal specimens was supervised by Professor J. Moojen. The collections assembled probably constitute the best collection of neotropical mammals from a single region. One card was issued for each specime caught. In these cards, information about environmental conditions reproductive state, ectoparasites, testing for plagues, and some of the animal's measurements, was written.

The material was collected over a large area (Fig. 3.1). Two natural domains exist in the region: the tropical atlantic forest and the caatinga. An intermediate belt of deciduous and semi-deciduous forests occurs between these two regions. I shall refer to these regions by their proper local vernaculars: "Zona da Mata", for the rain forest, "Sertao" for the Caatinga mainland, and "Agreste" for the intermediate belt. The climate is distributed roughly in the same way as the vegetation. The seasonal distribution of rainfall is different in the Zona da Mata to the Sertao, the Agreste in general having the same rain season as the Zona da Mata. As the distribution of rainfall is somewhat irregular in the Agreste, this region in Bahia has a situation which is quite distinctive from the Agreste region in Alagoas and Pernambuco. Therefore, I lump the samples by region as follows

A. Zona da Mata/Agreste - Samples from the coastal rainforest of Alagoas and from the transition belt of Alagoas and Pernambuco.

B. Agreste, Bahia - Samples from the intermediate belt in Bahia.

C. Sertao - Samples from the Caatinga domain in the States of Ceara, Paraiba, Pernambuco and Bahia.

The samples were collected between 1952 and 1956. Data

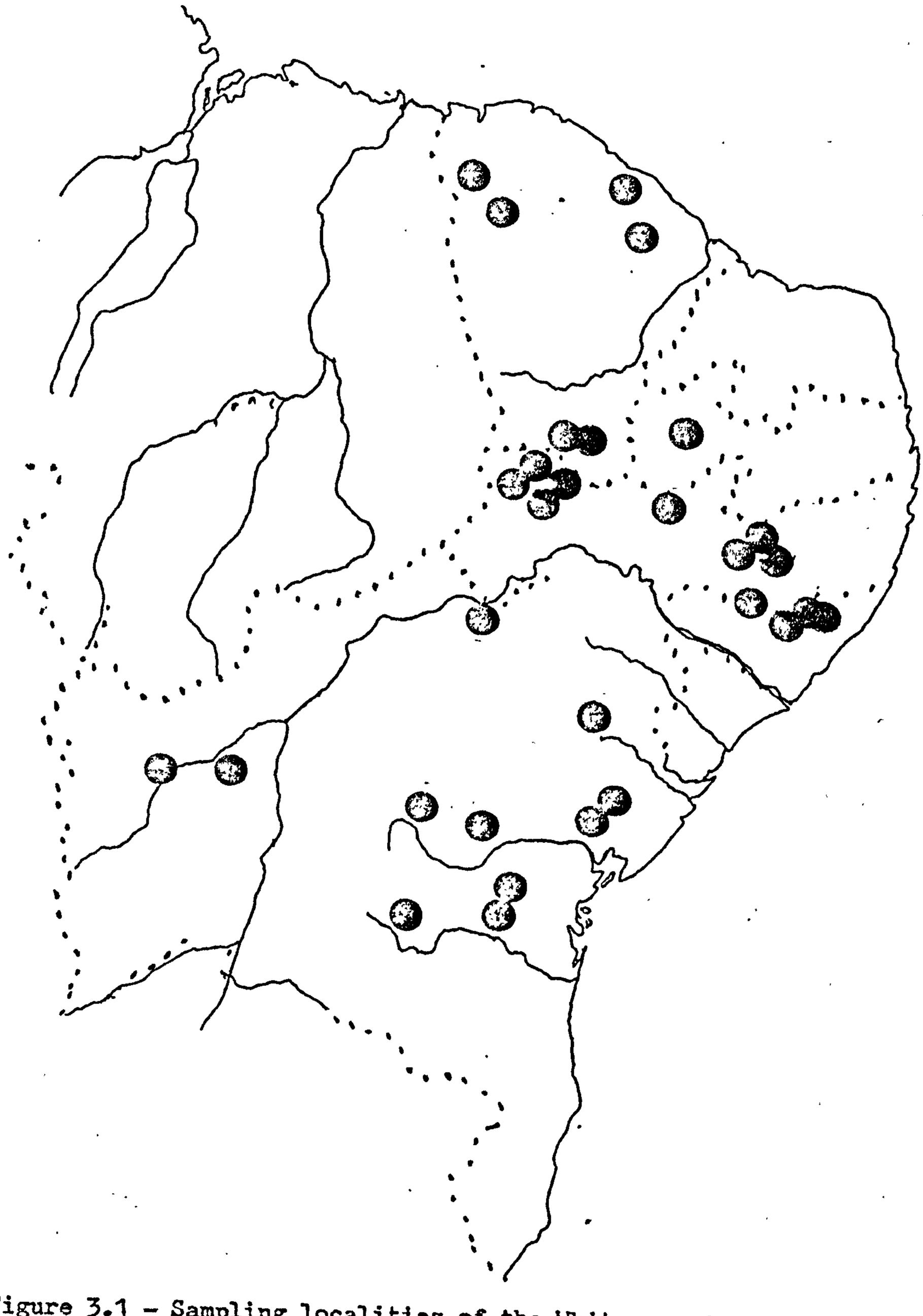


Figure 3.1 - Sampling localities of the White-eared Opossum in Northeastern Brazil.

from 662 specimens was examined. Of this total, only 318 specimens had skins and skulls examined. The rest, 344 specimens, have only their record cards, the actual specimens were not found or were not preserved. All specimens have their record card deposited in the Museu Nacional, Rio de Janeiro.

The animals were assigned to one of seven dental age classes. I sued for that purpose the system devised by Gardner (1973) as modified by Tyndale-Biscoe and Mackenzie (1976). I could not use the measurements from the record cards when the specimen was not examined due to the impossibility of assigning the specimen to such age classes.

Since not enough material was gotten from any single locality, I had to lump several samples as described above. The distribution and names of the localities are given in figure 3.1. Additional geographic information can be found in Appendix I.

3.A.2 Breeding Season and Litter Size

3.A.2.1. Males - The field collectors examined the testicles of all males captured and noted if these organs were vascularized or not. Vascularization increases during the breeding season. Therefore its presence can be considered as indicative of the reproductive condition of the male.

In figures 3.2; 3.3; and 3.4 the months which males with vascularised testicles are shown. For the three regions it appears that there is no correlation between rainfall and fertile males. Notice that in the Sertao (region C), there are fertile males all year long.

Figure 3.2 - Breeding Season in the "Zona da Mata/Agreste". (Region A):

a-Rainfall at intersection of paralel 8°S and ordinate 36°

(Source: BRASIL.Ministerio da Agricultura,1969)

b-Litter Size (Average)

c-Condition of vascularization of testicles

d-Occurrence of individuals of age classes 0,3 and 5.

e-Possible breeding seasons, deduced from the data above.

Obs.: (Breeding considered as matings, gestation and birth, but not lactation and weaning)

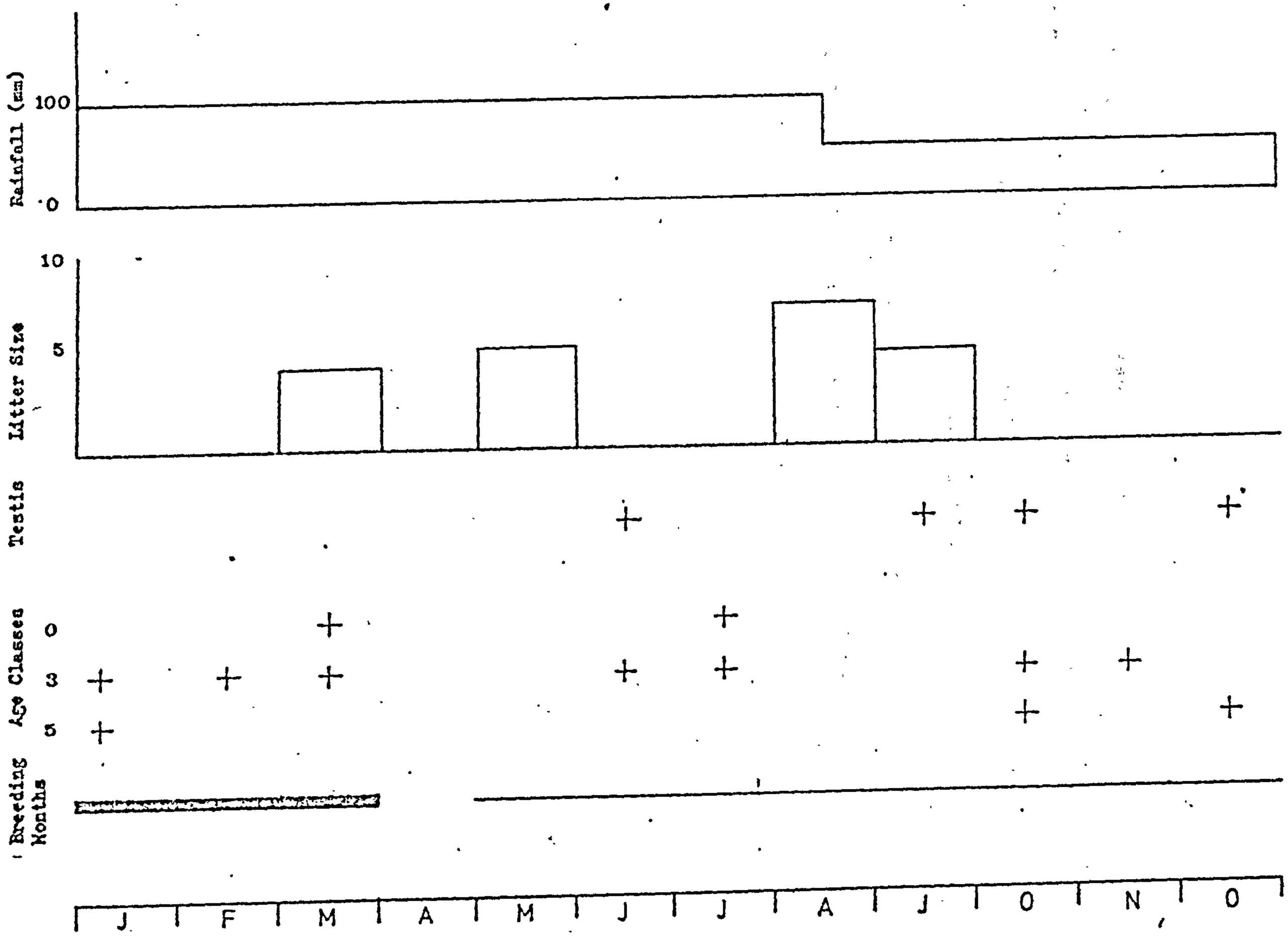

Rainfall (mm)
100
0
Litter Size
10
5
Testis
Age Classes
0
1
2
Breeding Months
J
F
M
A
M
J
J
A
J
O
N
O

Fig.3.2

Figure 3.3 - Breeding Season in the "Agreste,Bahia"(Region B)

a-Rainfall at intersection of paralel 12°S and ordinate 40°W.

(Source: BRASIL.Ministerio da Agricultura, 1969)

b-Litter Size (Average)

c-Condition of vascularization of testicles

d-Occurrence of individuals of age classes 0,3 and 5

e-Possible breeding seasons, deduced from above
(see obs. p/ p. 2)

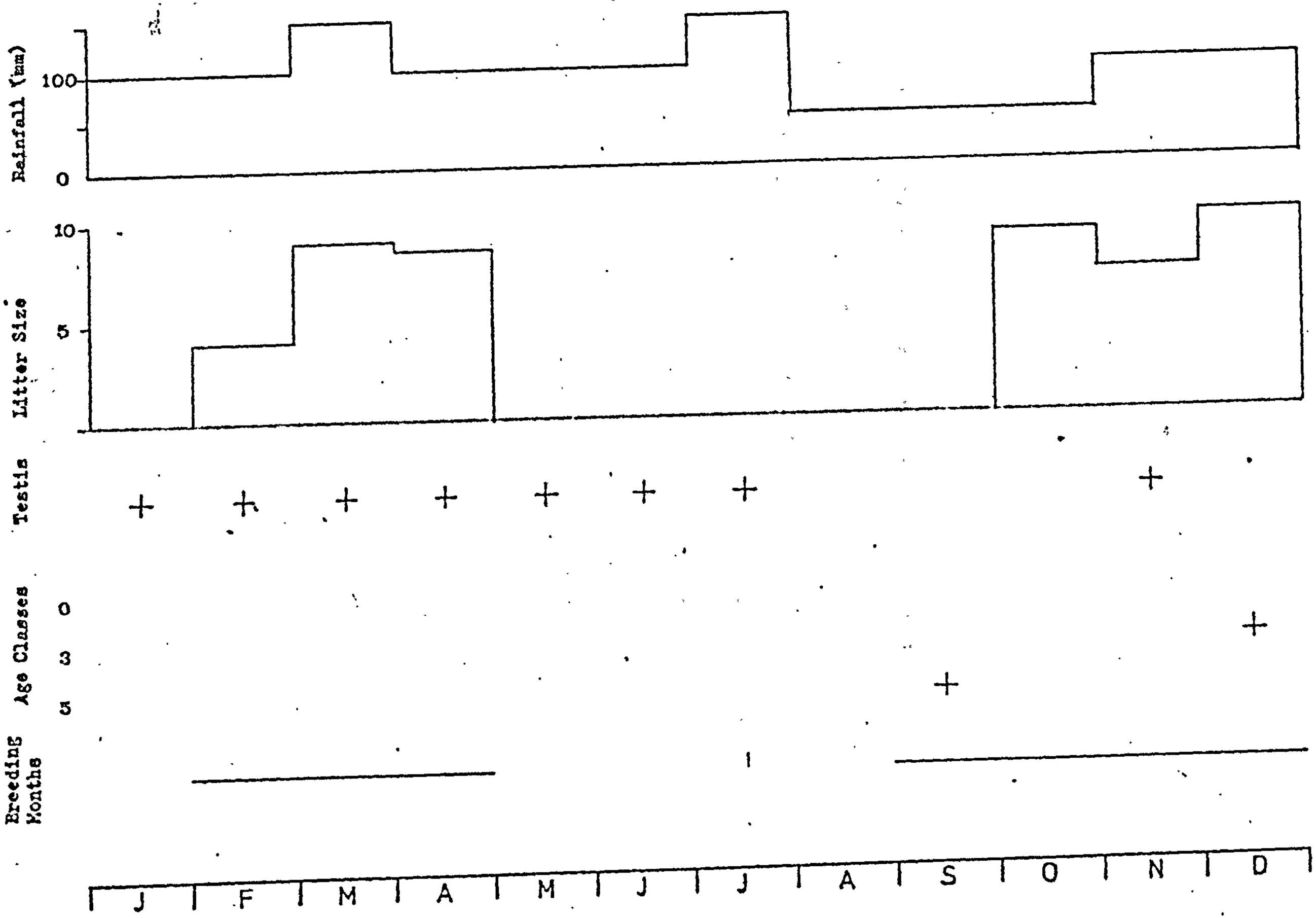

Rainfall (mm)
100
0
Litter Size
10
5
Testis
Age Classes
0
3
5
Breeding Months
J
F
M
A
M
J
J
A
S
O
N
D

Fig. 3.3

Figure 3.4 - Breeding Season in the "Sertao" (Region C)

a-Rainfall at intersection of paralel 8°S and ordinate 40°W

(Source: BRAZIL.Ministerio da Agricultura, 1969)

b-Litter Size (Average)

c-Condition of vascularization of testicles

d-Occurrence of individuals of age classes 0,3 and 5

e-Possible breeding seasons, deduced from above data.

(Ju 6b f' 8 3.2)

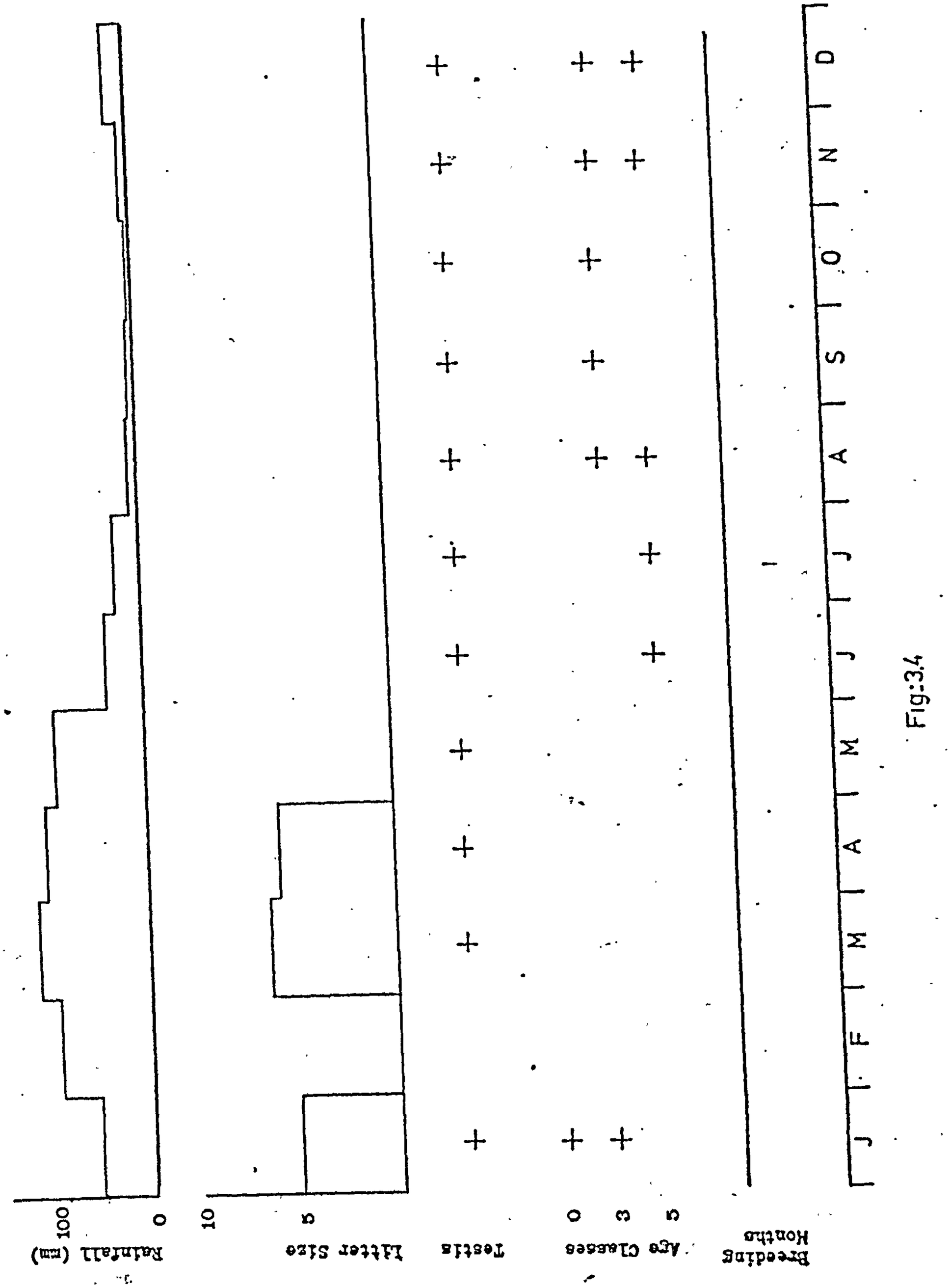

Rainfall (mm)
100
0
Litter Size
10
0
Testis
Age Classes
0
3
6
Breeding Months
J
F
M
A
M
J
J
A
S
O
N
D

Fig:34

3.A.2.2 Females - No data about the oestrous cycle was collected. The SNP field workers recorded the existence of embryos in the womb. This data is shown in figures 3.2, 3.3 and 3.4. Infant individuals of age class 0 are newborn individuals which were caught with the mother. The time of capture of these infants is also shown in the above-mentioned figures.

The combination of data above embryos and newborn infants gives an idea of the breeding season. In region A (Zona da Mata/ Agreste) the breeding season can be inferred to start about March. This time of the year is the beginning of the rain season. For region B (Agreste, Bahia) no newborn infant was seized. This region has a system of atmospheric circulation which causes two rain seasons every year (Nimer, 1977). The data suggests a rough correspondence between the rain season and the breeding season, the second rain season being with less pluviosity than the first. However, the amount of data is too small to be conclusive. The Sertao (region C) has a marked rain season. No pregnant female was found outside the rain season in the Sertao. (Figure 3.4).

3.A.2.3. Litter Size - 324 females of all age classes were examined for embryos in the womb. The findings were recorded on cards. Only 32 specimens had embryos. The technique used does not allow mortality to be noticed in the uterus, nor the number of ovula and the survival of pouch young. The conditions in which the counting of embryos was made was such that I presume some females with embryos were recorded as having none. The number of specimens examined with embryos is too small to analyse geographical or seasonal variations.

The average number of embryos was 6.5 ± 2.4. For each region, the mean number and standard deviation were respectively: A (Zona da Mata/Agreste) - 5.0 ± 1.2; B (Agreste, Bahia) - 8.5 ±2.0; C (Sertao) - 5.8 ± 2.2. The largest number recorded was 11 and the smallest 3.

3.A.2.4 Discussion - There is no common breeding season among the reginns studied. However, the breeding seasons of the females overlap. The correspondence between female breeding season and amount of rainfall suggests that the oestrous is environmentally controlled. If this suggestion is correct, temporal and spatial variation exist in the number of embryos, number of fertile females, etc. Years without rain in the Sertao probably see a smaller number of embryos being produced in the area and localities where there is permanent water and higher content of atmospheric moisture may have this number higher.

This variation enables the rapid recolonization of areas where local extinction had occurred. The rain forest regions will always have infants being born. The rainforest refuges inside the Caatinga domain will have high population, as well. Due to the structure of Didelphis populations and the high vagility of the opossum, these animals can always be present, local extinctions being only a temporary setback.

At the same time, it appears that Didelphis males in the Northeast of Brazil have individuals able to copulate any time among the population. Biggers (1966) studied D. virginiana in North America and D. marsupialis in Middle America and concluded in a similar way that " males do not experience a period of total

sexual quiescence." With females having the fertility environmentally controlled and males always fertile, whenever water is available, reproduction will occur.

3.A.3 Growth and Fertility

3.A.3.1 Weight and litter size - Tables 3.1 and 3.2 summarize the data correlating litter size with weight and age classes. The lowest weight with which a female was found pregnant was 226 g. Table 3.1 was composed using a pool of record cards with and without specimens. The data about growth (q.v.) shows that the average weight at age classes 5, 6, and 7 ranges between 457.0 to 607.9. Thus, higher average litter size is expected to fall between 450g to 600g. It i sometimes supposed that large mothers have higher numbers of children. However, even the incomplete data at hand (Table 3.1) suggests that the contrary is true in D. albiventris. Females with more than 850g were captured but none was pregnant.

The variation in the litter size is high in the tables. The cause is that the table is pooled with specimens from a large area and collected in different seasons. However, it is clear that there are more pregnant females in the range which corresponds to the mean of adults than among females with higher and lower weights. The data about low weight females came almost all from cards which have no specimen preserved. Therefore correlations between weight and age in the present section was done by inference and must be taken cautiously. I do not know if the female in the bottom of weight classes was a small adult or a precocious adolescent.

The number of pouch young may be slightly lower than the recorded embryos number.

Table 3.1

Correlation between litter size and weight of females in Didelphis albiventris Northeast Brazil.

WEIGHT (grams)	N	EMBRYOS MEAN	STANDARD DEVIATION	RANGE
201-250	1			5
251-300	5	5.2	1.1	4 - 7
301-350	1			7
351-400	3			4-5-7
401-450	4	9	0	9
451-500	3	4	0	4
501-550	5	8.2	3.0	3 - 11
551-600	3			7-9
601-650	6	5.8	2.7	3 - 10
651-700	2			4 - 10
701-750	2			3 - 4
751-800	0			
801-850	1			10
total	36	6.5	2.4	3 - 11

Table 3.2

Correlation between litter size and age class of females in Didelphis albiventris Northwest Brazil

AGE CLASS	N	MEAN	STANDARD DEVIATION	RANGE
0 to 4	none			
5	4	5.8	2.2	4 - 9
6	7	5.9	2.8	3 - 10
7	1			3
total	12	5.6	2.5	3 - 10

Classification of ages according to Tyndale-Biscoe & Mackenzie, 1976

3.A.3.2 Age Classes and Pregnancy - Table 3.2 summarizes the data correlating age classes and number of embryos. No female was found pregnant under age class 5. If the calculations made by Tyndale-Biscoe & Mackenzie (1976) are correct, then the females can be pregnant at about 10 months of age.

The litter size is almost the same in all classes considered. The value of $\underline{t}$ 0.5 = 1.73 (N = 48) when the average number of embryos in the totals of tables 3.1 and 3.2 are compared. At this level the difference between the means is not significant. Therefore, I can accept the null hypothesis of the difference between the mean of 11 females and the means which came from females which could have been assigned to age classes. This test gives reliability to the data in table 3.2.

Reynolds (1952) discussed the minimum and maximum breeding ages. He found six months as the earliets age in which breeding occurs in D. virginiana. He found no correlation between age and the time in which females began to breed. This absence of correlation is due to the methods used by Reynolds. He pointed out that no matter the time of birth, the female is capable of breeding in the beginning of the next breeding season.

The data I have for D. albiventris suggests that in the Northeast of Brazil, only adults breed. However the evidence I have gathered is not conclusive. The difference between the two species if real, may be due to the fact that in temperate regions there is no shelter for adverse winter as there is for some populations in Northeast Brazil. Therefore, the offspring must be reared before the winter. As it appears that local populations of D. albiventris regulates breeding reacting to local environmental conditions,

they can breed and rear their offspring when conditions are suitable. As consequence, the females can wait until they get the adult life when their size and weight have reached the region of the median of the local populations.

3.A. Sex Ratio

The pooled sex rate for all ages was 48.16 / 51.84 . For that rate, the χ^2 is χ^2 = .14 (N = 625) which falls in the range of 70% probability. (Null hypothesis)

PART B

DISTRIBUTION

3.B.1 Introduction

During the course of this research, I have examined a large number of individuals collected in localities. The data I have obtained enabled me to plot a detailed distribution map (Fig. 3.5). However, only this map is not sufficient to understand the causes of this distribution. In this chapter, I shall try to analyse what the factors which determine the occupation of space by Didelphis are in South America.

In order to study the distribution of this genus I have analysed two sets of data: the first came from the collecting cards that exist in the Museu Nacional, Rio de Janeiro, and refered to D. albiventris collected in Northeast Brazil. The other set is composed by climatic, vegetational and other characteristics of the environment of each collecting locality. To obtain the data for this second set, I used the literature on climate, Botany

and Bio-geography of South America. A secondary source is the bibliograph on Didelphis Ecology.

The nature of the data I have does not allow me to determine the detail of the habitat where Didelphis actually live. Therefore, in general, only macro climatic and macro-vegetational classifications were used.

These shortcomings were unavoidable in the scale of the work. However, since the intention was not to detail the ecology of the opossum, but to understand its distribution, I think the data obtained is sufficient. In some few cases I tried to give more detail. These cases I have called the limit cases of distribution. The analyses of such cases was very useful to get an insight into the general pattern.

The chapter is organised giving first the empirical evidence, altitudinal, climactic, etc. At each point I prefered to discuss the immediate implications of the findings, constructing the argument for the following parts. After these evidences, I used the concept of morphoclimatic domain (discussed in chapter two and appendix one) as a useful summary. After that the discussion of some limit cases closes the points for the argument, and general conclusions are discussed.

In the first chapter, the present taxonomic status of Didelphis was presented. This classification agrees well with the major ecological divisions of the Neo-tropical Region. First, there is a basic division between the forest and open area forms, the form for the first herein called the Didelphis marsupialis group, the latter the Didelphis albiventris group. The D. marsupialis group inhabits the ensemble of rain forests of South America

I shall use the name Didelphis marsupialis for the population living from the Amazonia to the north, and Didelphis aurita for the populations of the Atlantic forest. The Didelphis albiventris group the white eared opossums (D. marsupialis being black eared), thrives on the continuous open area which comes from the Northeast Coast of Brazil to the Monte Desert in Argentina, through the Caatinga, the Cerrados, the Chaco up to the Monte. For this population, the name Didelphis albiventris albiventris is used. Populations living in the Andes are called Didelphis albiventris azarae. The future taxonomic status of the Didelphis marsupialis group is discussed in Chapter five.

3.B.2 Altitudinal and Latitudinal Distribution

Map Fig. 3.5 shows the distribution of both forms of Didelphis in South America. The white eared opossum ranges from about 10° latitude North to about 40° latitude South. Unfortunately I could not examine samples South of Buenos Aires. However, the Southern limit is based in Mares (1976) who found Didelphis in the Monte Desert.

Hershkovitz (1969) has identified specimens collected in Roraima and in the Gra-Sabana as D. albiventris, where it occurs isolated from the rest of the other populations of the same form, the nearest region where the white eared opossum occurs being at some600 kilometers distance.

The D. marsupialis group has its populations divided by a large gap, in my records by about 800 kilometers through the Brasilian Highlands and by about 1400 kilometers in Northeastern Brazil.

Figure 3.5 - Distribution of Didelphis in South America

● Black Eared Opossum (*D. marsupialis* group)

○ White Eared Opossum (*D. albiventris* group)

The records in the figure came from direct examination of specimens.

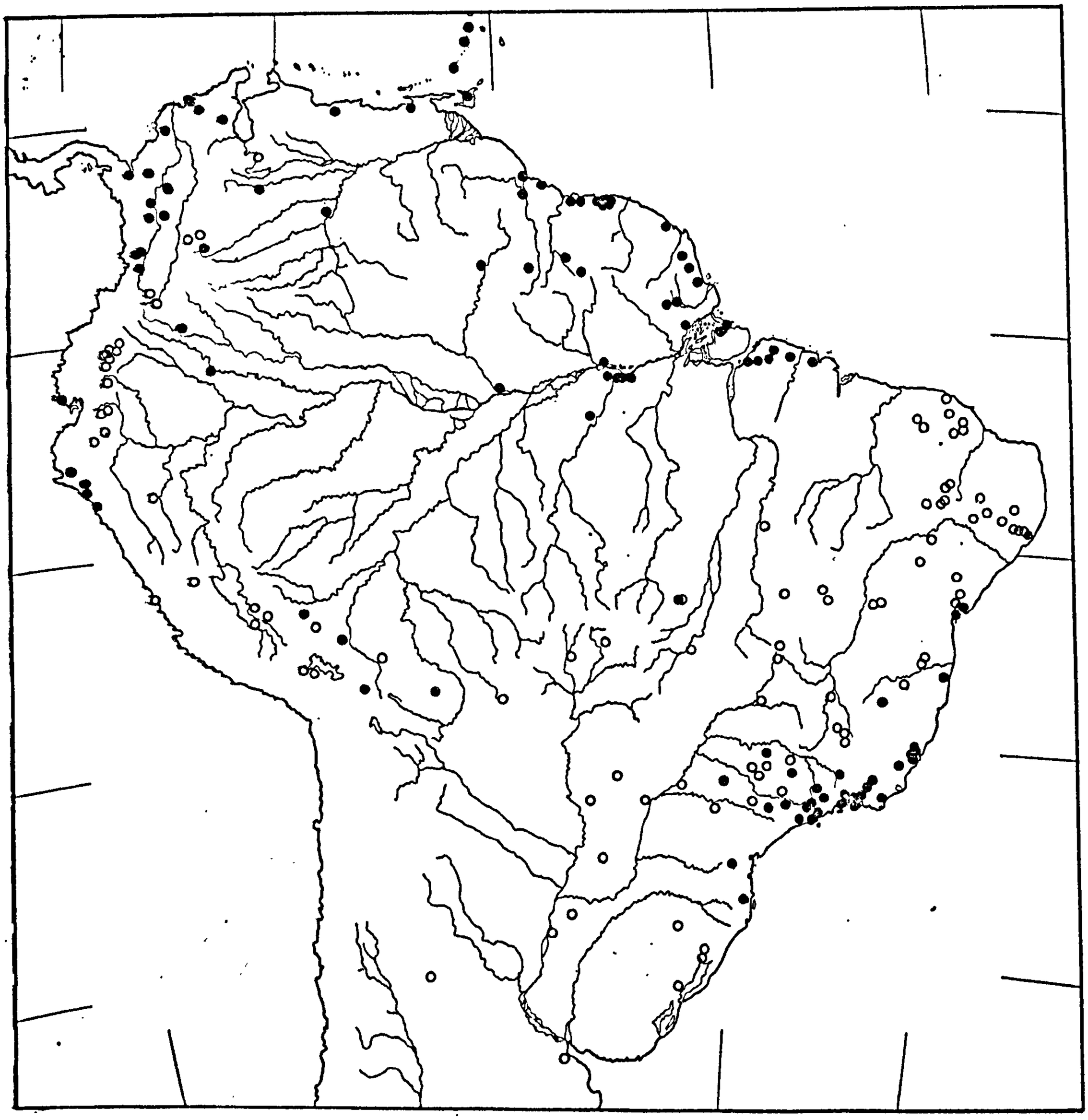


Figure 3.5

Figure 3.6 - Scatter Diagram: Altitudinal and Latitudinal Distribution of Didelphis in South America

■ D. aurita

□ D. marsupialis

◉ D.a.albiventris

○ D.a.azarae

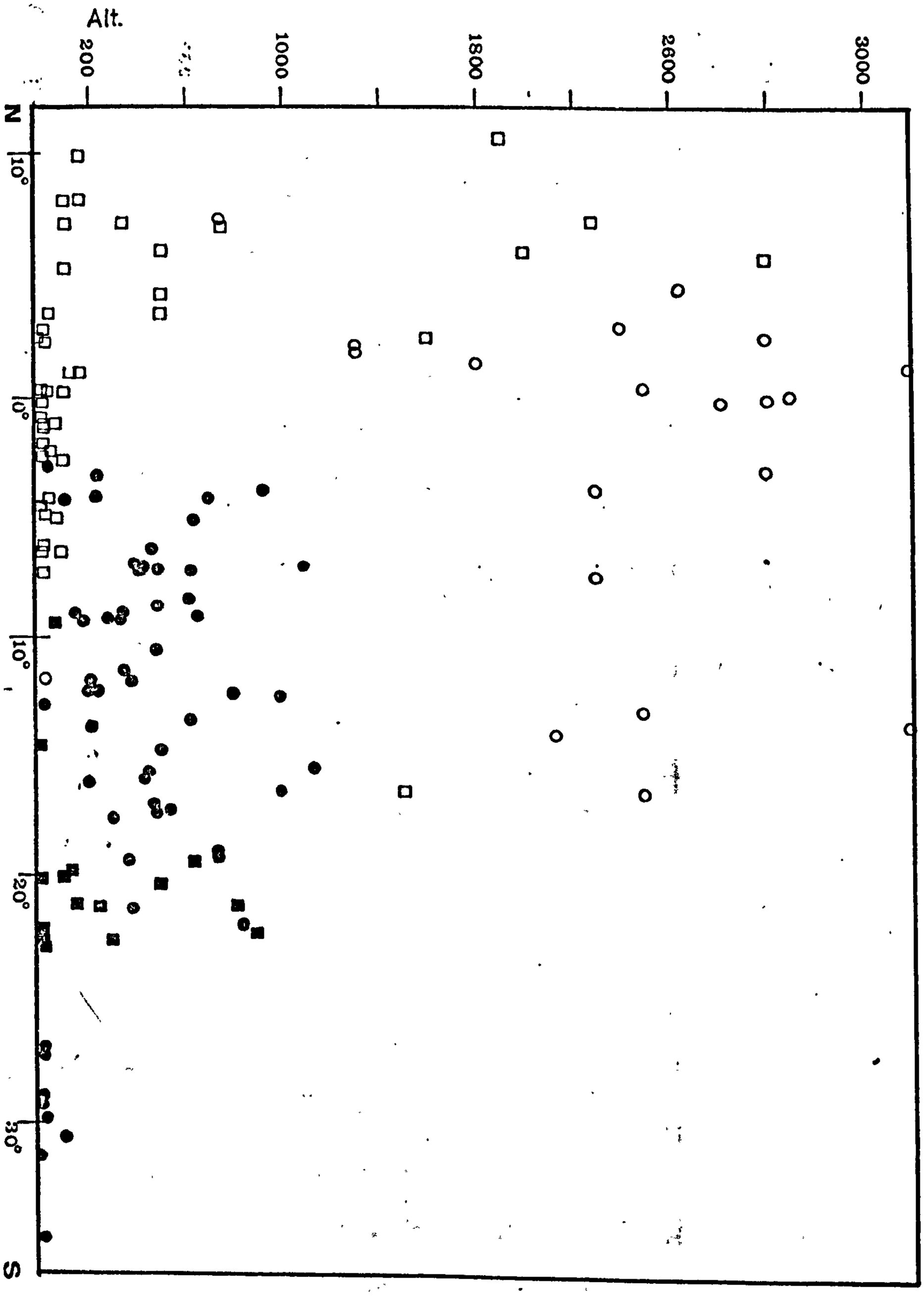


Figure 3.6

The two forms are not usually found in the same place. An expedition of the Royal Society /Royal Geographical Society has collected them in the same locality in the Brazilian Highlands. In Sao Paulo State, the two forms constitute a mosaic, some places with one form, some with the other. These limit cases are discussed below.

It is usually said (e.g. Hershkovitz, 1969; Hunsaker, 1977) that "D. albiventris" is a middle altitutde and latitude species. In order to test this assumption I have plotted in a graph (Fig. 3.6) the altitudinal and latitudinal distribution of Didelphis in South America. D. marsupialis occur in the same latitudes as D.a. azarae. Of course the first extends north, through the Central America, the latter is restricted to the Andes. Azarae is restricted in altitude. But marsupialis overlaps its altitudinal range with azarae. Notice that, in general, their localities do not coincide.

D.a. albiventris extends farther South than aurita. But, again, in the same latitudes the distribution of both species has nothing to do with altitude. Only D.a. ~~aurita~~ azarae has therefore a rigid altitudinal limit.

3.B.3 Climate

3.B.3.1 Temperature - I have got the annual average maxima, minima and mean temperature of the collecting localities of Didelphis. Table 3.3; 3.4; and 3.5 show the range of these average temperatures of each of the four forms. From this data it seems that all the populations occur only when the mean temperature is above 15°C with the exception of D.a. azarae. This form has the lowest upper

limit as well.

D.a. azarae lives in the place with the lowest average minimum temperature. For the average maxima this form has the shortest range and lower values.

Notice that for these three temperatures, D. aurita and D.a. albiventris have similar ranges.

3.B.3.2 Precipitation - Both forms of the D. albiventris group can occur in areas with very low rainfall. The D. marsupialis group is restricted by rainfall averaging less than 1000mm/yr of total precipitation (table 3.6). However, there are two records, one in Ecuador and the other in Colombia for D. marsupialis where the average rainfall is respectively 285 mm/yr and 291 mm/yr.

3.B.3.3 Cloudness - D.a. albiventris is the only form which occurs in areas with low cloudness (table 3.7).

3.B.3.4 Effective Precipitation Index (Thornthwaite) - The Thornthwaite index relates precipitation with the mean temperature The index values shown in table 3.8 are the sum of average monthly values. There is a relationship between this index and the type of vegetation. The classification of types is shown in Fig. 3.8. This is related to the relationship established, which indicates the actual water available for the vegetation after evaporation is taken into account.

Didelphis in South America splits in two groups in relation to this index. The D. albiventris group which ranges from arid to super-humid areas and the D. marsupialis group which is restricted to humid and super-humid areas. However, there are some populations of this group which inhabits areas with a very low effective precipitation, as low as 0.84 (Lambayeque, see T.3.11)

Table 3.3

Ranges of Average Annual Mean Temperature of Didelphis Collecting Localities in South America

Didelphis albiventris albiventris	-	15.8°C	- 26.0°C
Didelphis albiventris azarae	-	6.0°C	- 22. C
Didelphis marsupialis	-	17.4°C	- 29.4°C
Didelphis aurita	-	16.3°C	- 25.6°C

Table 3.4

Ranges of Average Annual Minima Temperature of Didelphis Collecting Localities in South America

Didelphis albiventris albiventris	-	9.8°C	- 25.2°C
Didelphis albiventris azarae	-	7.7°C	- 12.8°C
Didelphis marsupialis	-	19.1°C	- 22.9°C
Didelphis aurita	-	10.7°C	- 25.0°C

Table 3.5

Ranges of Average Annaul Maxima Temperature of Didelphis Collecting Localities in South America

Didelphis albiventris albiventris	-	22.0°C	- 34.0°C
Didelphis albiventris azarae	-	20.6°C	- 22.3°C
Didelphis marsupialis	-	30.6°C	- 33.7°C
Didelphis aurita	-	23.3°C	- 30.0°C

Table 3.6

Ranges of Annual Average Total Precipitation of Didelphis Collecting Localities in South America

Didelphis albiventris albiventris	-	311.7 mm/yr - 1691.0 mm/yr
Didelphis albiventris azarae	-	565.3 mm/yr - 2000.0 mm/yr
Didelphis marsupialis	-	1238.0 mm/yr - 4307.0 mm/yr
Didelphis aurita	-	1044.0 mm/yr - 2408.0 mm/yr

Table 3.7

Ranges of Average Annual Cloudness (in tenths) of Didelphis Collecting Localities in South America

Didelphis albiventris albiventris	-	3.6 - 7.0
Didelphis albiventris azarae	-	6.3 - 7.5
Didelphis marsupialis	-	4.0 - 7.0
Didelphis aurita	-	4.6 - 7.2

Table 3.8

Ranges of Average Annual Effective Precipitation Index (Thornthwaite) of Didelphis Collecting Localities in South America*

Didelphis albiventris albiventris	-	16.0 - 128.0
Didelphis albiventris pernigra	-	31.6 - 96.4
Didelphis marsupialis marsupialis	-	85.9 - 144.2
Didelphis marsupialis aurita	-	64.0 - 159.1

*Localities in the Pacific Coastal Desert not included

3.B.3.5 Monthly Rainfall - The distribution of rainfall during the year is an important ecological factor. I too the average number of months during the year with rainfall above 100 mm, between 100 mm and 30 mm, and below 30 mm. D. albiventris group has the largest range of variability. The D. marsupialis group is restricted to areas with a rather regular distribution of rain, with a maximum of four dry months (table 3.9). This regularity is better seen in Fig. 3.7, which shows the position of the collecting localities in relation to the annual distribution of rainy months.

3.B.3.6 Interim Discussion - The data I have sued came from meteorological stations. Therefore, they do not give an accurate idea of both the movement of the atmosphere or of the microclimates in the region.But, they are in variation through the year and in their normality, indicators of the position of the places in relation to the air masses. At the same time, they indicate the limits of microclimates that can occur in the region.

The data analysed above shows that there are differences in what climatic conditions different populations of Didelphis live. In order to summarize this data I tried to use the Koeppen system of climate classification which is shown in table 3.10. Fig. 3.8 shows a scatter diagram relating cloudness to effective precipitation. The form I have called D.m. marsupialis is restricted to tropical climates, but it has some exceptions in the records I could get. All these exceptions are exceptional (in relation to the majority of localities of this form which have been considered) in the records of precipitation and in the index of effective precipitation.

Table 3.9

Number of Rainy/Semi-Dry/Dry Months in Didelphis localities in South America

	RAINY	SEMI-DRY	DRY
Didelphis albiventris albiventris	0 - 12	0 - 10	0 - 8
Didelphis albiventris azarae	0 - 8	2 - 11	0 - 8
Didelphis marsupialis	4 - 10	0 - 5	0 - 4
Didelphis aurita	4 - 11	1 - 8	0 - 4

RAINY MONTHS - Rain more than 100 mm

SEMI-DRY MONTHS - Rain more than 30 mm and less than 100 mm

DRY MONTHS - Rain less than 30 mm

****

D. aurita occur in similar conditions in the Tropical Atlantic Domain. However since it extends its distribution below the Tropic of Capricorn, it occurs in warm temperate climates as well.

D.a. albiventris occur in all major classes, i.e. Tropical savana, Rainforests, Dry steppe, etc. (table 3.10). Desert climates do not appear in my records. However, they occur in harsher conditions, as in the Monte (Blair, et.al., 1976), where the climate is arid and cold. This is the southernmost limit of the form and of the genus.

D.a. azarae, occuring only in the Andes, is restricted to temperate climates, in spite of the fact that most of the populations live above the Tropical line. There is in my records a locality with a dry steppe climate (Keoppen's BS). This class of climate is widespread in the Andes, several Andean valleys being very

dry (Hueck, 1972).

A scatter diagram relating nebulosity and effective precipitation is shown in figure 3.8. The points are somewhat displaced upwards due to the fact that I have not complete sets of data for all localities. Nevertheless, it is clear that a high humidity is an important condition for D. marsupialis group. Nebulosity, when related to orography, is indicative of the conditions of evaporation near the ground. It is used here since I believe it gives one an idea of the behavior of the air masses with the local. It is a good indicator of the kinds of forest one can expect. Therefore, in general, Didelphis thrives in areas with somewhat high humidity. There are exceptions:D. albiventris group inhabits dry places, as in the Monte and some Andean areas. The D. marsupialis group has populations in the Pacific Coastal Desert and in the Guajira region, in the Caribbean Sea, but those are marginal populations. D. albiventris has not only the above-mentioned arid areas as exceptions in its distribution, but for the whole area occupied by it, the humid condition is dryer than for D. marsupialis.

Table 3.10

Koeppen's Classification of Climates of Didelphis Collecting Locations in South America. Number of Localities Recorded for each Major Type (Number in brackets - number of localities classified for each form)

	A				B		C		
	Af	AW	As	Am	BS	BW	Cf	CW	CS
Didelphis albiventris albiventris (71)	-	27	8	4	10	-	9	12	1
Didelphis albiventris azarae (7)	-	-	-	-	1	-	-	6	-
Didelphis marsupialis (35)	5	4	-	20	1	5	-	-	-
Didelphis aurita (40)	7	11	-	3	-	-	6	13	-

But how is it that there are overlaps between the two groups? The point is that the microclimate found in different regions is determined by the interaction between climate and vegetation, climate, orography and soil interacting to determine what kind of vegetation is to be found in each place. I have no data on microclimates of Didelphis but differences can be infered from the interactions mentioned above. Climate (in the sense of macroclimate) alone can not explain the distribution of the opossums. Therefore I shall try to use some more environmental parameters to understand that.

3.B.4. Environmental conditions other than macroclimate

3.B.4.1 Conditions in Northeastern Brazil - Table 3.11 lists the environmental conditions where D. albiventris were collected in this region. Some animals had been trapped, others shot or caught by hand. Plants related to these conditions could not always be determined.

a. Shelter - The Cassacos (local vernacular for Didelphis) used to sleep during the day. They usually shelter for that. Some were caught in trees, the record not indicating the exact conditions. Usually the shelter they use protects them from conditions outside the shelter. For instance, they have been caught in bird nests, especially kinds of nests that are large with thick walls and a small opening (T.V. Barret, personal communication). Barret informed me that these dens have temperature and humidity which is steady during the entire day.

Other common shelters have been Bromeliads. These plants have a characteristic of maintaining a steady state of humidity (and temperature). They form a special kind of micro-

habitat (Picado, 1913), where several other organisms live. They conserve a constant supply of water. Decaying ~~lives~~ leaves remain under the plants for a long time, forming a natural den where Cassacos are frequently found.

The other shelters are similar in the steady conditions of humidity and temperature. Therefore, during the resting time, the Cassacos avoid problems of thermoregulation and water balance.

b. Kinds of Vegetation - Cassacos inhabit all kinds of vegetation that exists in Northeastern Brazil, from Caatinga to the Rainforest. When compared with other mammals in the region, the Cassacos seem to have a higher ecological tolerance. Most of the mammals in the Caatinga Domain live restricted to some areas, where water is permanent. Didelphis on the other hand, can live in the Caatinga itself, while Rodents, for instance, are almost non-extant in the Caatinga, being restricted to the "Brejos" and some woodland areas (Baltazard, 1968; Cerqueira, 1976). The Cassacos, judging from the data I have (see table 3.11) suit any kind of vegetation or plantation.

Table 3.11
Environmental Conditions where Didelphis albiventris Specimens Were Collected in Northeast Brazil

i. Shelter
Arvore - Unspecified tree
Cajueiro - Cashew tree (Anacardium occidentale, Anacardiacea)
Jaqueira - Jackfruit tree (Artocarpus heterophyllus, Moraceae)
Oco de Pau - Hollow tree
Touceira de Bambu - Bamboo thicket (Poaceae)

Cerca de Cama - Shrub fence

Cerca de Pedra - Rock fence

Moita de Murta - Murta thicket

Moita de Sao Goncalinho - Sao Goncalinho thicket

Tronco de Brauna caido - Fallen Brauna Tree

Touceira de Gravata - Bromeliad (Bromeliacea) thicket .in the ground .in trees

Furna de Pedra - Rock cave

Serrote de Pedra - Rock mound

ii. Kinds of vegetation

a. Natural Vegetation

Brejo - Marsh

Caatinga

Carrasco - Dense Caatinga, with thorny plants

Campo - Meadow

Mata - Forest (unspecified)

b. Crop Plantations

Algodao - Cotton (Gossypium spp., Malvaceae)

Banana - Musa spp. (Musaceae)

Batata - Potatoes, usually common potatoes (Solanum tuberosum, Solanaceae), but may be used for Sweet Potatoes as well (Ipomoea batatas, Convulvulaceae)

Cana de Acucar - Sugar Cane (Saccharum spp., Poaceae)

Feijao - Beans, Phaseolus spp (Fabaceae)

Mandioca - Cassava (Manihot esculenta, Euphorbiaceae)

Milho - Maize (Zea mays, Poaceae)

Palma - Thornless cactus (Cactaceae)

Brejo cultivado - cultivated marshland

c. Particular kinds of Vegetation

Mata de Cipo - Forest with high density of Vines and Lianes. Usually secondary growth forest or forest between two biomes

Capinzal - High grass

Capoeira de Macambira - Bromeliad coppice, Usually abandoned field of Sisal plantation.

Caatinga de Porco - Local name for a kind of thorny Caatinga

Caatinga em Lajeiro - Caatinga growing on rocky, flat surface

Mandacaru, Candeia, Facheiro, Xique-xique - Vegetation with a high density of one of these cacti (Cactaceae)

Junto a Catolezeiro - Near a wood of Catole Nut trees (Arecaceae)

iii. Terrain

Solo Pedregoso - Rocky soil

Solo Argiloso - Clay soil

Solo Arenoso - Sandy soil

Solo Plano - Plain soil

Solo Ondulado - Ondulated terrain

Lajeiro - Flat rocky surface

Tabuleiro - Low tableland

iv. Water

Periodic water

Permanent water

Near River

Near Wheel

Dry Caatinga

Source : Data deposited in Museu Nacional, Rio de Janeiro

****

c. Terrain and Water - Perfunctory statements about soil and availability of water are found in the collecting cards. These statements are listed in table 3.11. As for vegetation it seems that no particular kind of terrain suits the Cassacos better. Direct availability of water does not seem to be necessary either. Maybe, Bromeliads is an important source of water for them, since these plants usually preserve water in their petioles, being a reservoir of water. It is not known whether the population in dryer areas are less dense than the ones in more humid parts.

3.B.4.2. Distribution by Morphoclimatic Domains - The concept of Morphoclimatic Domains is very useful when dealing with large-scale problems of distribution. I tried to assign each collecting locality of Didelphis in South America to one of such domains.

Between and around some domains there are intermediate and fringe belts. These belts have complex elements, sometimes two rainy seasons a year, mosaics of different kinds of vegetation, etc. The patterns are very difficult to analyse. However, in such belts limit-cases of distribution are found. The varied habitat contains Fauna and Flora which are partially derived from the adjacent domains, partially their own.

The domains where each form of Didelphis were caught are listed below (cf. Appendix I: there is a brief description of all domains in South America).

Didelphis albiventris albiventris - Tropical Atlantic, Cerrados, Caatinga, Chaco, Coxilhas, Umid Pampa and Monte.

Didelphis albiventris azarae - Equatorial Andes, Puna, Paramo.

Didelphis marsupialis - Amazonia, Equatorial Pacific, Guajira, Pacific Coastal Desert, Equatorial Andes, Sierras Tucumano-bolivianas.

Didelphis aurita - Tropical Atlantic, Araucaria Highlands

Hershkovitz (1969- 1970) declared that specimens collected in the Gran-Sabana (Roraima and Auyan-tepui, but not in the Guianas) belong to the Didelphis albiventris group.

D.a. albiventris is found in the following intermediary belts: Bahia (between Caatinga, Tropical Atlantic and Cerrados) Parana Valley (between the Coxilhas, the Chaco, the Araucaria Highlands, and the Umid Pampas), Chaco Oriental (between the Parana Valley, the Cerrados, the Chaco, the Araucaria highlands and

the tropical Atlantic Domains), between the Cerrados and the Tropical Atlantic Domains in the State of Minas Gerais, in the Pantanal de Mato Grosso (between the Cerrado and the Chaco), in the Maranhao and Piaui States (between Amazonia, Caatinga and Cerrado) and between Amazonia and the Cerrados).

D. marsupialis was collected in the belt between Amazonia and the Cerrados, in Beni (between Amazonia, Chaco and Equatorial Andes), in the Guiana Fringe (the coastal plain surrounding the Amazonia, from the mouth of Amazonas to Venezuela). D. aurita was caught in the Chaco Oriental, in the Parana Valley, in Bahia and in the belt of Minas Gerais.

These domains can be divided into three groups: Domains where open vegetation is dominant, where forests are the chief vegetation and the oreal domains in the Andes. D.a. albiventris is found in areas of open vegetation. D. azarae in oreal areas. D. aurita and marsupialis in forest areas. The point is that when the concept of Morphoclimatic domain is used, it became immediately clear what are the climatic conditions for each form, high humidity by rain being essential to the maintenance of forests over a large area, oreal vegetation being limited upward by temperature savana usually by alternance of rainy and dry months over a latosol etc. Therefore assigning the Didelphis to Domain we have an almost complete picture.

3.B.5 Some Limit Cases

Some limit cases for which data is available are analysed below.

3.B.5.1 Pacific Coastal Desert - The Pacific Rainforest extends continuously in a lane from the Uraba Gulf to the North of Ecuador in the coastal plain. In the mountains there is altitudinal zonation, rainforest occuring as well in the lower altitudes, being gradually substituted by other forms of altitude forest.

From about 1^{o} North, the Rainforest is substituted by a Seasonal Tropical Forest, still a humid biome, occuring in the foothills of the Andes, and in the slopes, the altitudinal zonation modifies as well, cloud forests occuring there. The coast has mangroves and the first spots of the Pacific Coastal Desert. In the Peruvian coast, starts the true desert, the Northern part being almost without vegetation near the coast, the vegetation being restricted to the river beds. When the mountains turn very near the sea, some Lomas are found and south of parallel 8^{o} South, the core of the Atacama desert begins. The altitudinal zonation is varied, low altitudes with the desert, above a xerophitic vegetation and above that, cloud forests. The cloud forests go only until about 6^{o}N, the vegetation of the Andes being more and more arid in character further South.

This picture is determined by the presence of the Humboldt Cold Stream. This stream interacts with the dry east side of the Pacific high pressure cell, increasing the aridity. In the north, the limit of the rainforest is the limit of the stream the area under its influence being disputed by the warm stream from the north. The Humboldt's Stream is responsible for the low

temperatures in the region, which are lower than the equivalent in other localities in the same latitudes. The interaction between the air mass and the cold water is also responsible for the continuous formation of fog (garua, in local vernacular). This fog is the only source of water for life in large parts of the desert. (Walter, 1971; Weberbaver, 1945).

The records I have for Didelphis in the region are all of the black-eared opossum but one of the white eared opposum. One locality is Ancon, in the Gulf of Guayaquil. Table 3.12 shows the normals of temperature and precipitation of Ancon and of nearby Guayaquil. The region where Didelphis was captured is extremely arid. However, the desert in Ecuador, is restricted to small strips near the coast line. Occurrence of Didelphis is therefore explained as a marginal occurence of them. Their populations may exist near streams during the rainy months and may become extinct sometimes. The animal belongs to the marsupialis group, which seems to be more demanding of water. But, as the desert of Ancon is surrounded by weter regions, where the conditions certainly allow only marsupialis to exist, any opossum captured from the region must be of this group.

Four other records for marsupialis came from Piura, Lambayeque, Eten and Pacasmayo, all on the Peruvian coast. In table 3.12, the normals for Lambayeque are shown. It is a drier place than Ancon. The other localities are all near Lambayeque being as arid as it is. From Callao, a port near Lima, a record of D. albiventris came.

How can such a strange distribution occur? Notice that (table 3.12) there is a decrease in rainfall and temperature.

Table 3.12
Temperature and Precipitation in Some Pacific Coast Localities

	J	F	M	A	M	J	J	A	S	O	N	D
Ancon (2°18'S-80°42'W)												
Temperature	25.5	26.6	26.7	25.0	24.8	23.8	22.3	21.4	21.6	22.0	22.8	23.8
	Mean - 23.9°C											
Precipitation	40.6	86.1	106.7	43.2	1.8	3.1	0.5	0.5	1.0	1.3	0.5	0.3
	Total year - 285 mm : Effective Precipitation Year - 9.5											
Guayaquil(2°8'S-79°53'W)												
Temperature	26.2	26.2	26.6	26.7	26.1	24.9	24.1	24.2	24.5	24.6	25.1	26.2
	Mean - 25.4°C											
Precipitation	201	276	240	168	32	6	6	1	0	2	1	22
	Total year - 955 mm : Effective Precipitation year - 47.31											
Lambayaque(6°42'S-49°54'W)												
Temperature	24.7	25.9	26.2	24.6	22.0	20.6	19.6	19.3	19.5	19.8	20.7	22.5
	Mean - 22.1°C											
Precipitation	1.4	3.3	11.5	1.5	1.9	.1	0	0.2	0.2	0.4	0.5	2.5
	Total year - 25.54 mm : Effective Precipitation - 0.84											
Lima(12°6'S-77°3'W)												
Temperature	22.6	23.5	23.1	21.1	18.9	17.0	16.2	16.1	16.3	17.2	18.7	20.9
	Mean - 19.3°C											
Precipitation	0	0	1	1	2	6	9	10	10	5	3	1
	Total year - 48 mm : Effective Precipitation - 3.19											
Arica(18°28'S-70°20'W)												
Temperature	21.8	22.1	21.3	19.2	17.5	16.5	15.6	15.6	16.3	17.5	18.8	20.6
	Mean - 18.6°C											
Precipitation	0	0	0	0	0	0.1	0.1	0	0	0	0	0
	Total year - 0.2 mm : Effective Precipitation - 0.01											

Sources: Acosta-Solis,1965;Cordovez,1962;Clayton & Clayton,1947;Weberbauer,1945.

This general trend is disturbed by the increase of fog formation in the mountains, responsible for the occurence of cloudy forest above the arid line up to parallel 6°. Looking in a lesser scale map (for instance the Map of Hispanic America), I noticed that all localities of marsupialis have a river nearby. These rivers came from the Andes, and have in the area a woody vegetation in their valleys. Water is permanent (the largest plantation of sugar cane in Peru is in one of such valleys (Hueck, 1972). Therefore, there are parts of the desert which can support Didelphis marsupialis just because these particular parts are not deserts! In spite of the almost ineffective precipitation. The increased aridity further South, together with lowered temperatures, causes the change in vegetation which impedes the occurence of the marsupialis group. As is discussed in the case of the Cauca Valley, the black-eared opossum inhabits the mountain vegetation up to some altitude and the coastal populations are off shots of the ones in the mountains. In latitudes south of 7° South, the only source of water being the garuas, and with decreasing temperatures, the vegetational belts of the Eastern slopes of the Andes have arid characteristics, only the populations of the D. albiventris group can live there. As the aridity further increases, Paramo being substituted by the Puna in high altitudes, in the Eastern slopes there will probably be no Didelphis at all. The record of Callao probably is one of the southernmost possible ones in the Eastern slopes, no matter the altitude.

3.B.5.2 The Valle del Cauca - This valley is inhabited by the D. marsupialis group in almost its whole length. The sourthernmost locality I have a record of being Popayan at about 1700 meters high.

The Lower Cauca Valley is covered by the Pacific Equatorial Rainforest.

In the Upper Valley, the vegetation belongs to the complex of the Equatorial Andes Domain. Some xerophitic enclaves are found in the valley. The interception of humidity by the Cordillera Occidental makes the lower valley more humid than the Upper valley, because moist wind counterbalances the influence of the Andes. Therefore, arid conditions are more frequent in some slopes of the upper valley. However, the altitude of the Cordillera Occidental allow some moisture to pass, river down the slopes being permanent, and the vegetation in general being similar to plant life in the lower valley. These conditions allow the existence of marsupialis in the region.

The temperature is not very low, well in the range of the D. marsupialis group. Apparently there is altitudinal zonation in the distribution of Didelphis. Excepting for the dry enclaves, the zonation of the vegetation is altitudinal, i.e., is temperature linked. I have a record of D. albiventris in the lower valley, together with marsupialis. As altitude changes a lot in few kilometers, I suspect the two samples came from different altitudes As a whole, the distribution of Didelphis in the Andes is determined by altitude, each species having preferential ones (see Fig. 3.5). My hypothesis is that having higher altitudes lower average mean temperatures and higher differences between maxima and minima temperatures, and having the D. marsupialis group populations restricted thermal tolerance, D.a. azarae displaces the other in higher altitudes.

D. marsupialis populations live in the continuous

forest that exists in the Valle del Cauca. This forest is interrupted sometimes, in the past by arid enclaves and some other vegetation and today by human interference as well. The forest climbs the slopes of both sides of the valley, marsupialis inhabiting all the forest. At some altitude, marsupialis is restricted by the lowering of temperature, and albiventris azarae is to be found. Excepting for the record in Callao, (see Pacific Coast), all azarae have been found in high altitudes (Fig. 3.5) this form being restricted for temperature as well. In the zone where both forms are in contact, it seems that the temperature is a set of factors that underlies competition.

3.B.5.3 Northeast Brazil - Didelphis aurita occur in a thin lane of rain forest near the coast of Northeast Brazil. The Northernmost record I have is a sample from Sao Miguel dos Campos, in the coastal plain of the State of Alagoas. Vicosa, in the same State, is only some 110 kilometers further in the mainland but in its fauna, D. albiventris occupies the opossum niche. The climatic conditions are very similar in both places, Vicosa having a more extended period of drought, while Sao Miguel has no month with less than 30 mm of rainfall.

A similar situation is found in the Reconcavo, the region around the Baia de Todos os Santos, State of Bahia. In the rainforest of the coastal plain, D. aurita is the form of opposum found. Some 100 kilometers further west, only D. albiventris is caught. Examining the climate and vegetation distribution in the area it is possible to understand Didelphis distribution.

The atmospheric circulation in the area is very complex due to the position of the region which is influenced by several

systems of circulation. The distribution of rainfall near the coast is quite regular during the year. The coastal plain is a thin lane between the uplands and the sea, being very rainy. From the coast toward the west, the rainfall drops. The vegetation is very sensitive to these conditions. The temperature is always high and therefore during some months in the mainland there is a deficit in the water balance. The types of vegetation in general changes from East to West, from Rainforest to Deciduous Forest. Further in the mainland is the Caatinga. Didelphis population follows this vegetational-climatic distribution, D. albiventris in the Deciduous Forest, D. aurita in Broadleaf Rainforest. D. albiventris can live in the more humid forest. For instance, there are some humid foothills in Ceara where the vegetation is a kind of Broadleaf Forest. In these areas the opossum is D. albiventris. On the other hand, D. aurita is limited by low humidity. Therefore the latter occupies only the continuous forest. The hypothesis here is that when the rainforest is occupied by aurita, this form excludes albiventris and albiventris excludes aurita when they come in contact in the Deciduous Forest. But why is aurita (or marsupialis) not found in the "Brejos" and humid foothills of the Caatinga Domain?

3.B.5.4 Cerrados in the States of Sao Paulo and Minas Gerais - The Tropical Atlantic Domain occupies the whole area of Sao Paulo. Scattered throughout the State there are several enclaves of Cerrados. The map Fig. 3.5 shows that the distribution of Didelphis in this State is a mosaic of albiventris and aurita. In Minas Gerais the same mosaic occur in the intermediate belt between the Cerrados and the Tropical Atlantic Domains.

Cerrado and Rainforest can occur in similar climate situations. Cerrado is determined more by soil than by climate. However, in regions of high rainfall, latossols can support a forest. On the other hand, if rainfall is low or if the forest disappears, the Cerrado can occupy the area. Open vegetation areas can be punctuated by forests, due in general to particular soil and or climate.

The analyses of vegetation of the localities where albiventris were recorded in Sao Paulo, shows that this form occurs in the Cerrado spots, aurita being the form of the forested areas. In Pocos de Caldas, Minas Gerais, aurita occurs in an apparently isolated spot, again, the region is forested, even occuring in a Cerrado area.

3.B.5.5. Serra do Roncador - An expedition to the Serra do Roncador, Mato Grosso, collected both D. marsupialis and D. albiventris in the same locality. The labels in the specimens indicate that albiventris was caught in the Cerrado and marsupialis in the Gallery Forest. The expedition has published some results on vegetation and soils of the region (Ratter, 1971; Askew et al. 1971).

The Gallery Forest fringes the rivers of the region, which is covered by Cerrados and by two types of Cerradao, Seasonal Woodland Deciduous Forest, the three types being characteristic of the Cerrado Domain. The floristic structure of the Gallery Forest is different from all the other types of vegetation. The region is climatic intermediate between Forest and Savan climates. The soils under the Gallery Forest are poorly drained, peaty, classified as hydromorphic soil.

The macroclimatic conditions being the same for both Cerrados and Forest, soils are determinant in the type of vegetation which occur. The microclimate will therefore be dependent on the vegetational cover and orography. In the.flood-plains there is permanent water, a very humid soil and a somewhat dense forest. In the other vegetation, Cerrado or Cerradao, the soil retains less water and the vegetation does not cover and get a high humidity inside. Thus there is a higher evaporation. Therefore, humidity conditions are quite different in each part, even with general climatic conditions being the same.

This is the sourthernmost record I have of D. marsupialis. The Amazonia is far away, but the Gallery Forest works as extensions of the Hyleae inside the Cerrados Domain.

3.B.5.6 Bolivian Andes - The distribution of Didelphis in Western Bolivia is interesting, some localities of D. marsupialis being more to the West than some of the D. albiventris azarae localities.

As a whole, the Andes have a very complicated landscape in some kilometers, the altitude rises sharply, the zonation being both latitudinal, longitudinal and altitudinal, frequently complicated by local landscapes which are different from the surroundings. In the Eastern slopes of the Andes, a continuous forest occurs, very varied from place to place, depending on local conditions. The Forest may be an Evergreen Forest or Deciduous, varying through Subtropical and Clout types of Evergreen Forests. The humidity is higher than in the corresponding slope in the West. The same applies for the temperature, which in general is higher than in the other side of the mountains. Altittude can be considered the chief factor in the environment, since it determines

the average temperatures. The position of the mountains from place to place is important as well, because it can cause differences in rainfall.

As in Colombia and in Peru, here again I found that D. marsupialis and D.a. azarae are limited by altitude. I do not have records of any climatic normal for the collecting localities I have recorded. But I can assume that temperature is the limiting factor for the distribution of each one of the opossums. My data does not allow me to know what exact compartiment of the landscape the samples I have were collected. Notwithstanding the above, the data clearly indicates that marsupialis is restricted to the slopes and valleys with Evergreen Forests, albiventris occuring in the lower parts of the Puna, more humid and probably in the Woods of Alnus ("Mata de Aliso") and Polylepis ("quenoa").

The accounts of Mammals of the Puna (Pearson, 1952; 1958; Hershkovitz, 1969; 1972) do not mention Didelphis as belonging to its Fauna. However, some locality records I have indicate that this animal occurs in the Domain, which must not be confused with the dominant vegetation. In general, it seems that the true Puna corresponds to the distribution of the Vicuna (Vicugna vicugna), (Koford, 1957). Comparing Didelphis records with the distribution of the former animal, it seems that the white eared opossum and the vicuna do not live in the same places.

3.B.6. Discussion

After the above summary of environmental conditions where Didelphis live in South America, it is clear that the two groups here considered, D. albiventris and D. marsupialis, corresp-

ond broadly to the type of vegetation, the former living in open areas, the latter in forests. For Didelphis forest means an Evergreen forest. Vegetation is an important way to understand what types of climate, soil and orography exist under it. However it is in itself a major ecological factor, the chief factor for Didelphis. But the play is set with temperature and the distribution of humidity throughout the seasons as well.

The analysis of what I have called limit-cases seems to be very rewarding, these cases being not the exceptions but the situation where the conditions which are extreme for each form appear more clearly. These limit cases set some questions as well. For me, these questions send us to the historical set which have led to the present day destribution. Let us now discuss these historical implications.

Didelphis occupies a broad niche, let us call it "the opossum niche" which seems to exist in almost every ecosystem North of Patagonia. Each form is a true vicarian of the others (in the sense of Croizat, Nelson & Rosen, 1974). The D. albiventris group has populations living in the continuous set of open vegetation formations which ranges from the Northeast Coast of Brazil to Patagonia. These formations have varying degrees of rainfall, humidity, water balance, temperatures, etc. Two offshots of D. albiventris occupy two other areas with similar vegetation, but both areas are better called Oreal than Open Vegetation, since it seems that altitude plays a major role in the character of the vegetation of these areas. They are the populations I have called D. albiventris azarae, in the Andes and the populations in the Guiana Shield. The Auyantepui is an almost unknown area

with but a few descriptions. I could neither examine any specimen nor get climatic data from this region. The little data I have about azarae indicate that this form lives in conditions which are rather different from the populations of lower altitutdes. Some populations of the so called D.a. albiventris live in the Monte Desert (Blair, et. al. 1976). In terms of temperature variation and humidity conditions, as well as vegetation, the Monte has several affinities with the Puna. However, it seems that the actual Puna is aovided by D.a. azarae. It gives us the situation whereby a set of populations is almost isolated geographically and ecologically from the others. The hypothesis is that the Andean populations have been isolated for a long time, since no route appears to have existed to link albiventris (s.s.) to azarae other than through the Monte. During dry periods they may have been more isolated than today. Therefore I think azarae has,possibly, a situation of separation from the other populations near or above the species level. I prefer to think that the split is not yet complete, more by parsimony than by evidence. One more evidence of the restricted ecological conditions of azarae is the fact that it is restricted to the Andes. During the glacial maxima this form probably lowered its altitudinal limits, following the same movement by the vegetation. However, azarae could not invade the Guajira, nor reach the Santa Marta Range in Northern Colombia or the Llanos del Orinoco, regions of Oreal or Open Vegetation where no albiventris is found today. This species must have been restricted for some time to the Oreal environments of the Andes, since it could not reach other places during the Glacial maxima, the last time there existed very favourable conditions for that.

The Didelphis marsupialis group is restricted to humid broadleafed forests. The populations in the Atlantic Tropical Forest are isolated from the ones in the Amazonia by some hundreds of kilometers. Is D. marsupialis the same species as D. aurita? While the D. albiventris group occupies the Opossum niche in a collection of kinds of vegetation, D. marsupialis seems to live in a more "homogeneous" environment. But actually, there is no such homogeneity in the rain forest of South America. The environmental factors analysed here do not allow a distinction between aurita and marsupialis as was found between albiventris and azarae. Therefore the status of the D. marsupialis group will wait further evidence to be discussed (cf. chapter four).

Apparently, Didelphis virginiana (Hunsaker, 1977) and D. albiventris (Barret, 1979), do not have a definite home range or territory. I think that what Hunsaker (1977) describes as the spatial distribution of individuals of virginiana applies for the whole genus. As any other animal, a minimum area must be available for the population of Didelphis to remain ~~extinct.~~ extant. Being omnivorous and medium sized (in relation to other South American mammals) and having a capability to wander through large areas, it seems that they can not be confined to very small areas. Albiventris has populations in the spots of Cerrado of Sao Paulo. But marsupialis do not occur in the similar patches of Broadleaf Forest of Ceara. This evidence suggests marsupialis is more sensible to environmental conditions, including minimum areas.

The enclaves of humid conditions in Northeast Brazil during a dry period must have to be smaller than today. The strip of Atlantic Forest in this region is a thin one near the coast.

During the Glacial maxima this strip was restricted as well. Marsupialis, if they ever lived in these enclaves, became extinct by this area reduction.

Barret (1977) has found only D. albiventris in Castro Alves region not far from the Coast in the Reconcavo of Bahia. The region has suffered the impact of human settlement in large scales since the XVI century. The forest is cleared off, the soil used for some time for crops, and the forest takes over again, to be cleared again some time later. There is no large forest in a continuous fashion in the area, only coppices of secondary growth. Barret has identified two kinds of vegetation, a humid one in the side of the coast and the "Agreste" vegetation further inland. Only D. albiventris has been collected in the area. This picture is on a small scale what has happened through environmental change in South America: small patches of forest are left surrounded by open vegetation and are invaded by albiventris, even if the environment inside the forest is more favourable to marsupialis. The area of forest can only support small populations of the latter and these are competitively excluded by the large ones of albiventris.

Similar events probably have taken place in the Cerrado, enclaves in Amazonia in which, I suspect, D. albiventris is non-extant. However, the gigantic enclave of open vegetation of the Auyantepui and Roraima has an area which is large enough to sustain its albiventris.

Competition is a phenomenon difficult to prove. The conditions in some humid enclaves of the Caatinga Domain are very similar to the ones in the Atlantic Forest. Similar habitats

have similar niches and the Opossum Niche in both forests favours marsupialis. Since marsupialis does not exist in the Humid Enclaves the Opossum niche was filled by albiventris. This is an indirect evidence of the competition which exists between the two forms, competition being a major factor in explaining the distribution which is seen today.

CHAPTER IV

GEOGRAPHIC VARIATION IN THE "DIDELPHIS MARSUPIALIS" GROUP

4.1 INTRODUCTION

This chapter will study the geographic variation of the Didelphis marsupialis group. As a preliminary step, correlations among all characters were calculated in order to avoid redundancy. After the characters had been analysed in this way, some of them were chosen to be studied seperately and others were studied by regression analyses.

Samples with larger numbers, here called major samples, were tested together and are presented here. After that, transects were studied. For reasons given in the text, the samples from Eastern Brazil were studied separated from the Northern South American ones. Summaries and interim discussions will appear when necessary.

4.2 CORRELATIONS AND CORRELATION PLEIADES

Figures 4.1 to 4.4 show the correlations between all characters in the major samples. It is considered that there are correlations pleiades between dimensions of some parts of an organism as well as absence of correlations between others (Berg, 1960). The chief objective in calculating the pleiades related to the studied characters was to see if some of them were redundant, since if two characters are significantly correlated it is better to consider them as being parts of the same ensemble and to consider them together (Mayr, 1969).

The problem here is what constitute "highly correlated characters". I have chosen the level of 5% and 1%, but there are

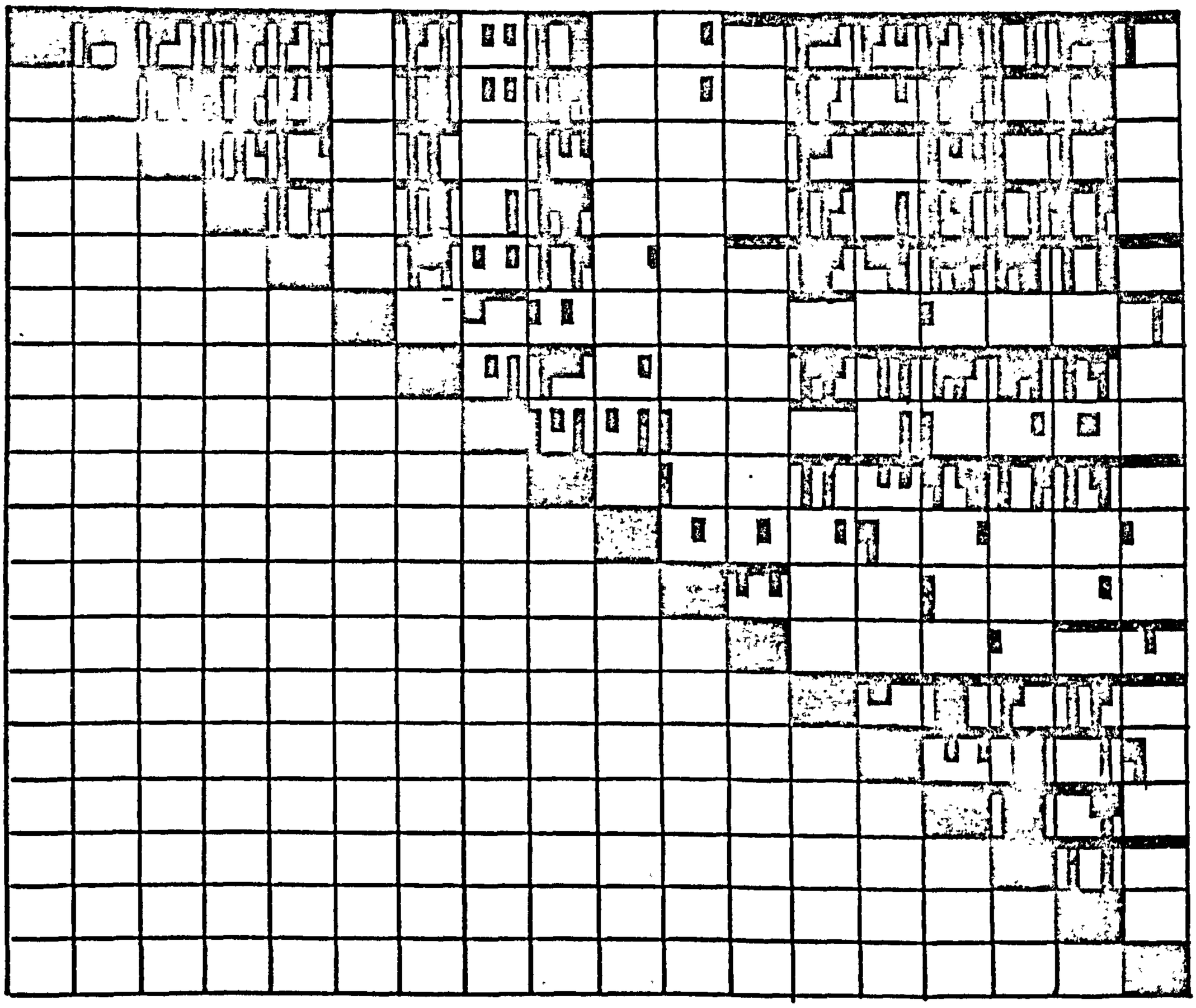


Figure 4.1 - Males Eastern Brazil. Correlations:

Horizontal Bars - Inter-locality Correlations

Vertical half Bars - Intra-locality Correlations at 5%

Vertical whole Bars - Intra-locality Correlations at 10%

Vertical Bars from left to right:

BFLM, COTM, ESPM, GBTM, ILIM, ZMMM

Axes labels as in fig. 4.3

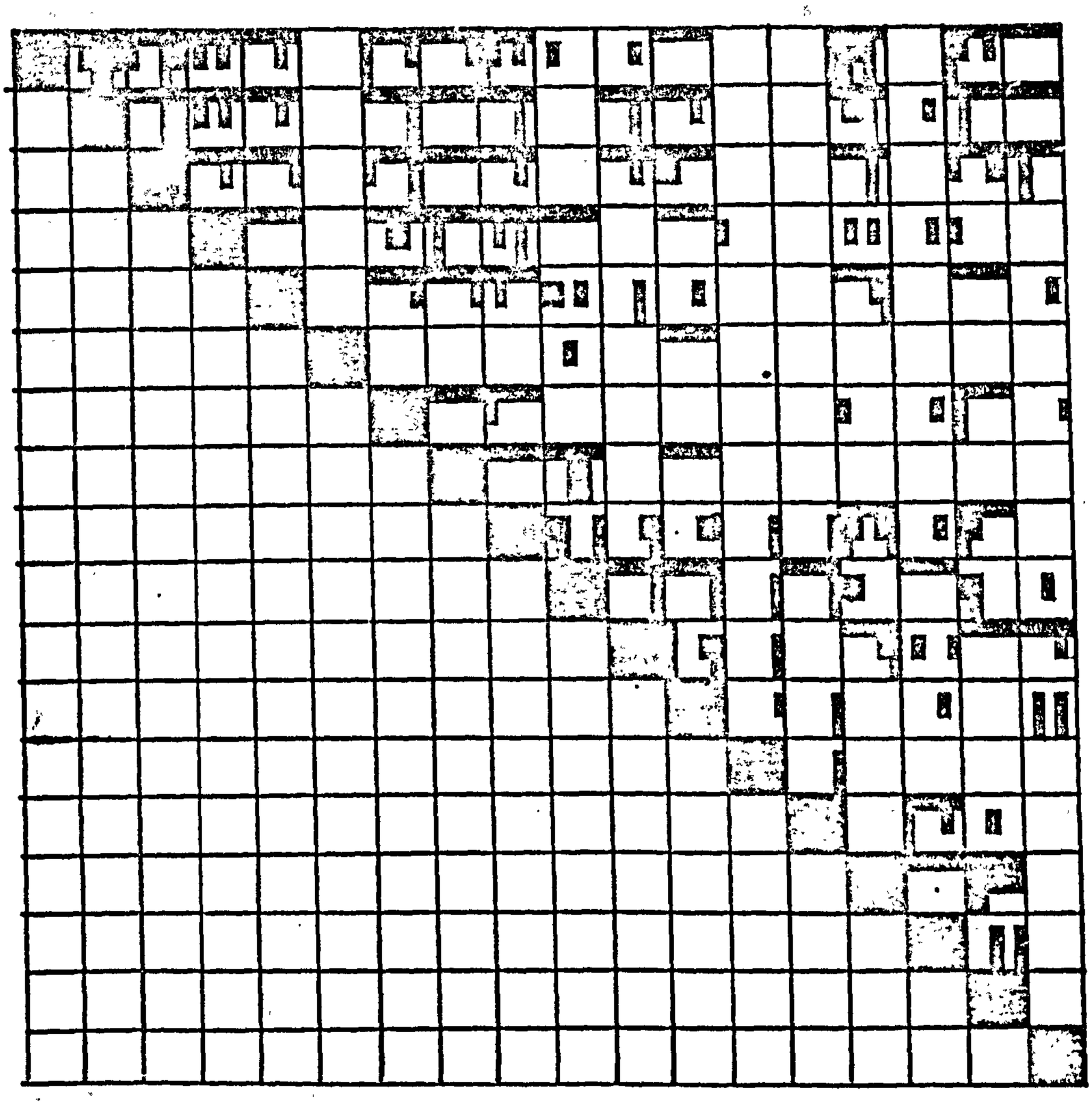


Figure 4.2 - Females Eastern Brazil. Correlations:

Horizontal Bars - Inter-locality Correlations:

Vertical half Bars - Intra-locality Correlations at 5%

Vertical whole Bars - Intra-locality Correlations at 10%

Vertical Bars from left to right:

COTF, BFLF, ILHF; LITF, TERF

Axis labels as in fig 4.3

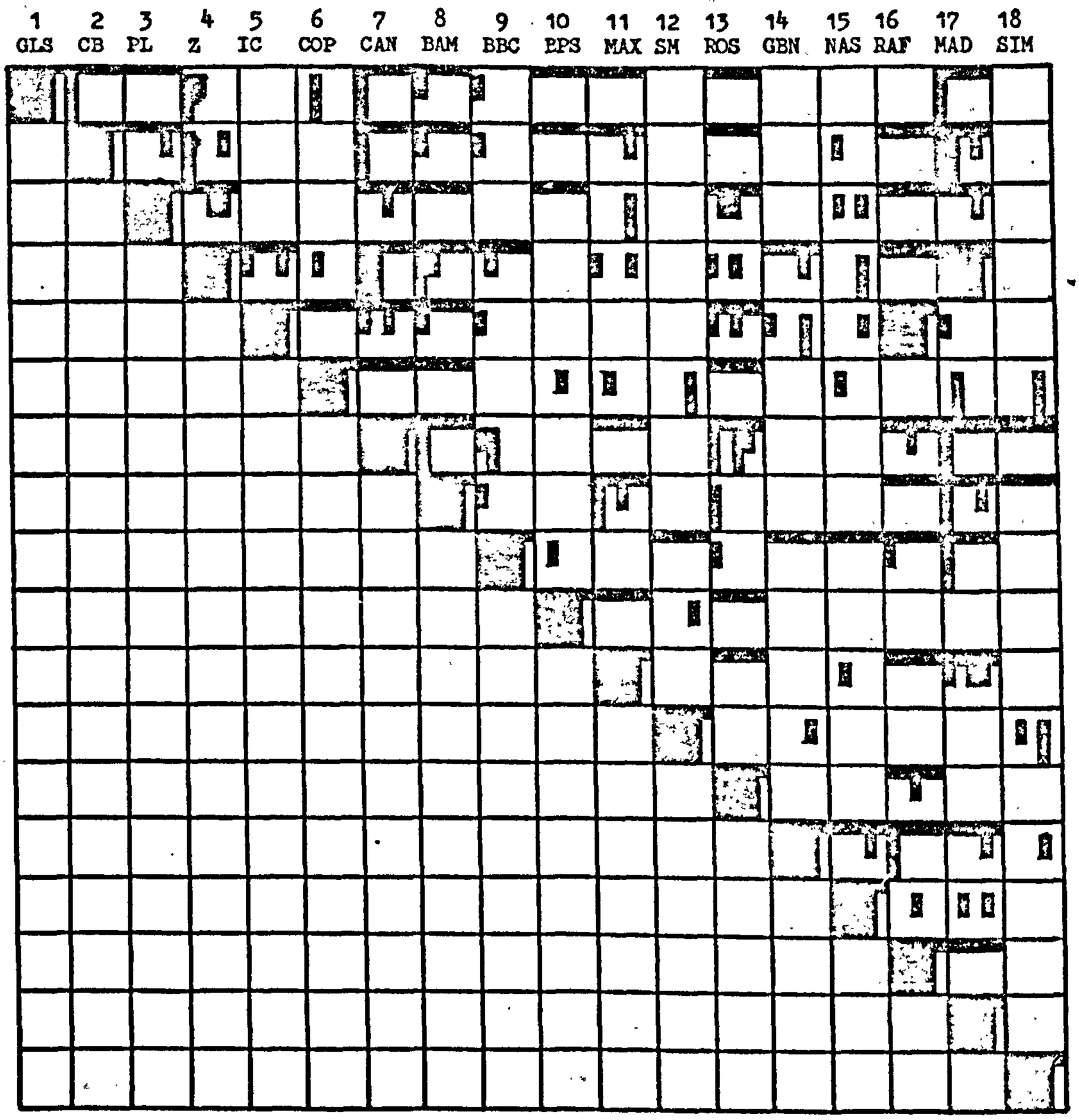


Figure 4.3 - Males Northern South America. Correlations:

Horizontal Bars - Inter-locality Correlations

Vertical half Bars - Intra-locality Correlations at 5%

Vertical whole Bars - Intra-locality Correlations at 1%

Vertical Bars from left to right:

SENM, STMM, SURM, BELM

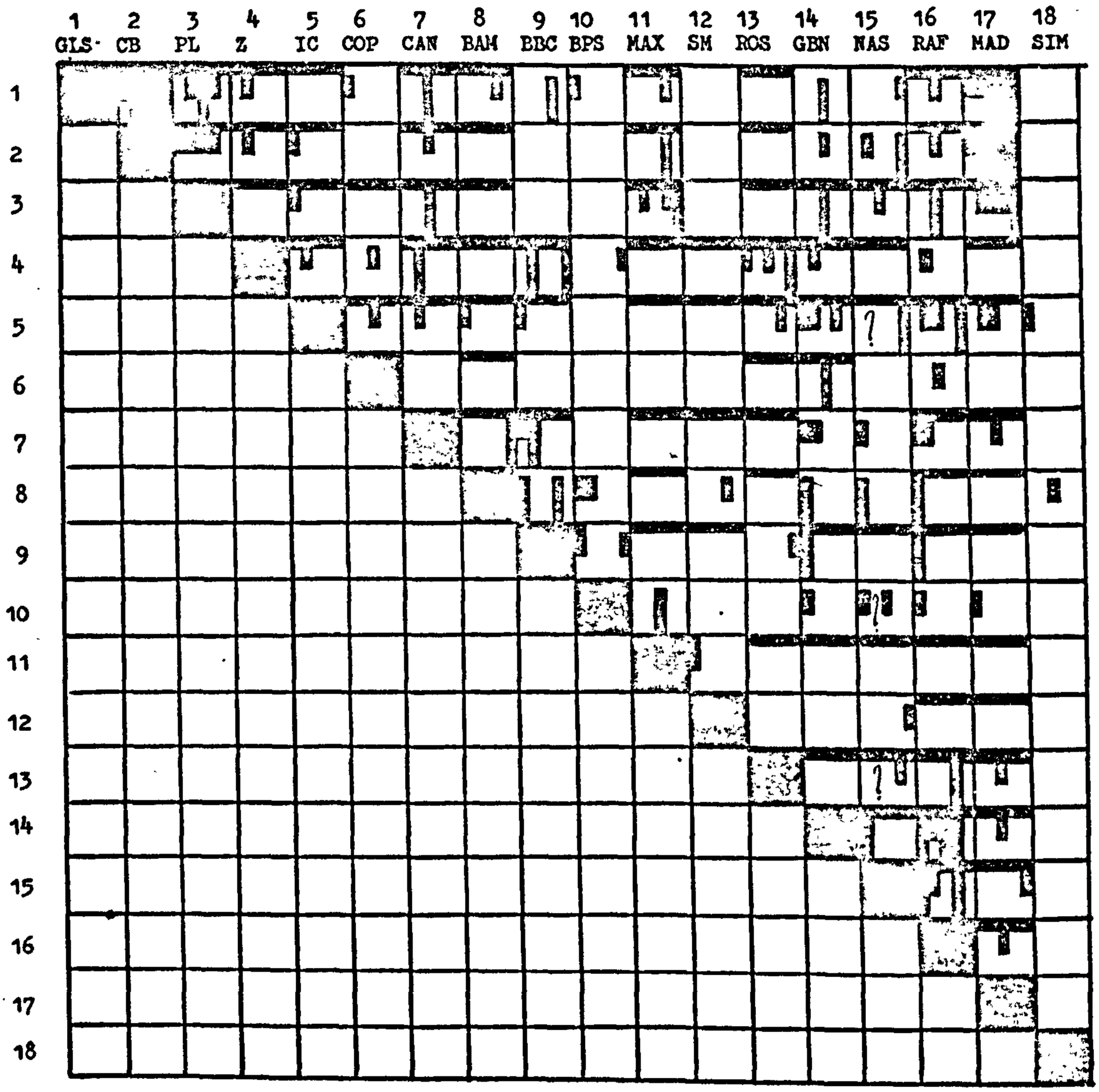


Figure 4.4 - Males Eastern Brazil. Correlations:

Horizontal Bars - Inter-locality Correlations

Vertical half Bars - Intra-locality Correlations at 5%

Vertical whole Bars - Intra-locality Correlations at 1%

Vertical Bars from left to right:

BELF; CALF, CURF, SENF, SURF

still the problems discussed in the introduction about the nature of the samples. At the same time, a decision had to be taken on whether a character had to be highly correlated in all samples or not to be considered as parts of the same genetical or functional system. I decided that if all or all but one locality had high correlation for a given pair of characters, the pair was considered as part of the same system. The correlation pleiades of correlated characters are shown in figs. 4.5 to 4.8. No further study was carried out and the characters were chosen just by inspection of these figures.

The following ensembles were considered among the males of Eastern Brazil: 1.GLS, MAD. CB; 2 CB, Z, BBC, NAS, IC. Notice that CB is part of both ensembles, which suggests that they have something in common. To recover information from these ensembles I decided to analyse MAD as an independent character and the pairs CB-Z and IC-NAS through regression analyses. The other characters which do not correlate in these ensembles are studied as individual characters.

Among the females in Eastern Brazil, Fig. 4.2 shows correlations in all samples. However, postérior calculations showed that there were arithmetical errors during the process of the computation. Since all regressions were by this time already made, and some correlations were still found among the variables, only CB was left to represent the correlations, instead of calculating all over again.

The males of Northern South America have three ensembles (Fig. 4.7). To recover information from these samples the following pairs are considered: IC-RAF; CAN-ROS; Z-MAD. CB is not used and

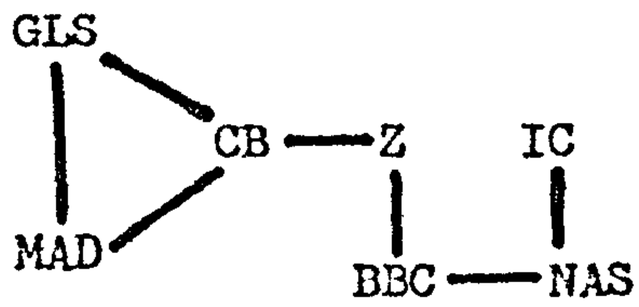


Figure 4.5 - Characters with high correlations in males of samples from Eastern Brazil.

Figure 4.6 - Characters with high correlations among females of samples from Eastern Brazil.

Figure 4.7 - Characters with high correlations. Males of North South America.

Figure 4.8 - Characters with high correlations. Females of North South America.

MAX is used as an independent variable.

Finally, the females of Northern South America show two ensembles and, even with some redundancy, the following pairs can be considered from fig. 4.8: CB-PL; GLS-MAD; GBN-RAF.

A point must be made here about these pleiades before going further: Males and females do not have the same pleiades and, populations from the Atlantic Forest (Eastern Brazil) are different in this arrangement in relation to their counterpart in the Amazonia (Northern South America). Mayr (1963) calles a drastic rearrangement in a given genetic system, a genetic revolution. Differences as the ones demonstrated here between correlation pleiades are, in my view, demonstrative of the existence of two separate specific entities, since I agree with Thorpe (1976) that the rearrangement of correlations can be considered as indicative of Mayr's genetic revolutions. Therefore, these two sets of populations (samples) are here treated seperately.

4.3 ENVIRONMENTALLY INDUCED VARIATION

Using the same data gathered for the study of the Ecology of Didelphis (see chapter 3), I could obtain some climatic data (Maxima and minima average temperature, means, annual rainfall and effective precipitation) for some localities of the D. marsupialis group in Brazil. The analyses were carried out for 10% of all characters of all four sets of samples. These characters were chosen at random. None was found to have relation with these environmental features. The method I used was to calculate values of correlation coefficients and multiple regression analyses. Regression coefficients between these variables and latitudes were

made and found not significant as well.

4.4 REGRESSION ANALYSIS

4.4.1 Eastern Brazil: Males

Two pairs of characters were analysed. The first one, Condylo-basal length and Zygomatic breadth (CB-Z) was tested by the F test and was found not significant. Regression equations and regression correlations coefficients, as well as results of the test are shown in table 4.1.

The second pair, length of nasals and Interorbital Constriction was tested by the F test and the result wa found to be significant. Table 4.2 shows the several equations. Figure 4.9 has the straight lines from these equations plotted. A second test was performed between neighbouring localities. The Zona da Mata de Minas sample (ZMTM) and Espirito Santo (ESPM) do not have significant differences. ESPM and Ilheus (ILHM) do not show significance either (Table 4.2).

4.4.2 Northern South America: Males

Three pairs of characters were analysed. The first pair is Z and MAD. The F test was significant at the level of 5%. Testing between the neighbours proved significant between Surinam and the other two. Table 4.3 and figure 4.10 summarize the findings

The second pair is IC and RAF. They were found to be non-significant among all samples. See table 4.4 and figure 4.11.

The last pair, ROS and CAN, have only two samples with enough specimens to analyse. There is no significant difference.

Table 4.1 Regression Analysis. Males Atlantic Forest.
Condylo-basal lenght (CB) - Zygomatic breadth (Z)
CB = x
Z = y

r's Critical values: * 5%;** 1%

Sample	Equation	r^2	r	n_i
SCAM	y = .80x + 27.11	.93	.96**	6
COTM	y = .76x + 21.33	.50	.71**	16
GBTM	y = .88x + 32.77	.96	.98**	7
BFLM	y = .64x - 5.70	.76	.87*	5
TERM	y = .56x - 2.35	.86	.92**	7
ZMMM	y = .48x + 7.56	.58	.76**	10
ESPM	y = .59x - 4.65	.75	.86*	6
ILHM	y = .60x - 4.69	.80	.90**	17
All samples	y = .58 - 2.59	.90	.95	74

$F_{7/58} = 1.8537$ n.s.

Table 4.2 Regression Analysis. Males Atlantic Forest.
Lenght of Nasals (NAS) - Interorbital constriction (IC)
NAS = x
IC = y

r's Critical values: * 5%; ** 1%

Sample	Equation	r^2	r	n_i
COTM	y = .45x - 1.80	.73	.85**	16
GBTM	y = .73x -14.83	.88	.94**	6
BFLM			.06 n.s.	7
TERM			.61 n.s.	9
BFLM + TERM	y = .59x - 6.90	.57	.75**	15
ZMMM	y = .43x - .65	.65	.81**	9
ESPM	y = .73x -15.82	.98	.99**	6
ILHM	y = .54x - 5.95	.79	.89**	18

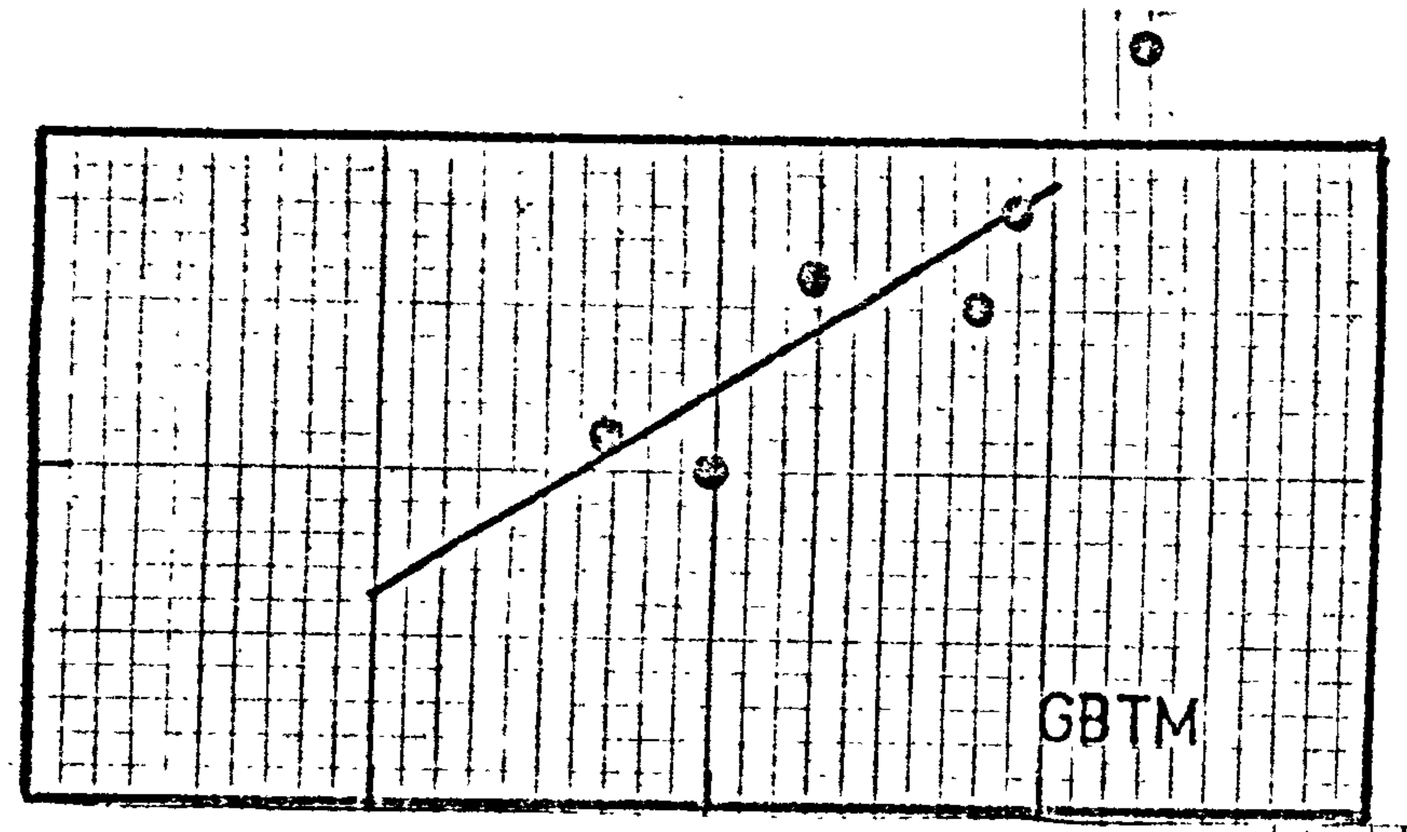
$F_{5/53} = 7.0787$**

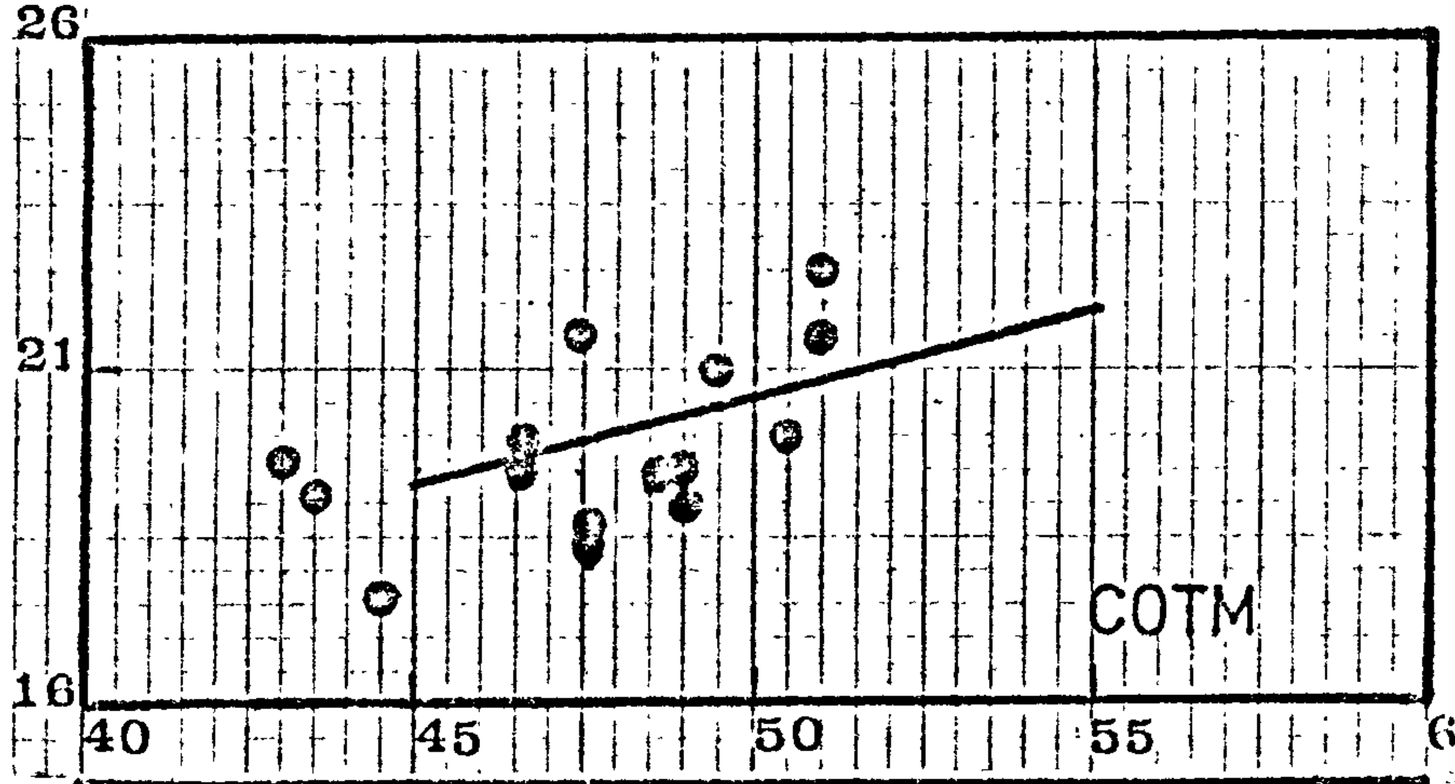
Vertical bar indicates non significant differences between the coefficients.

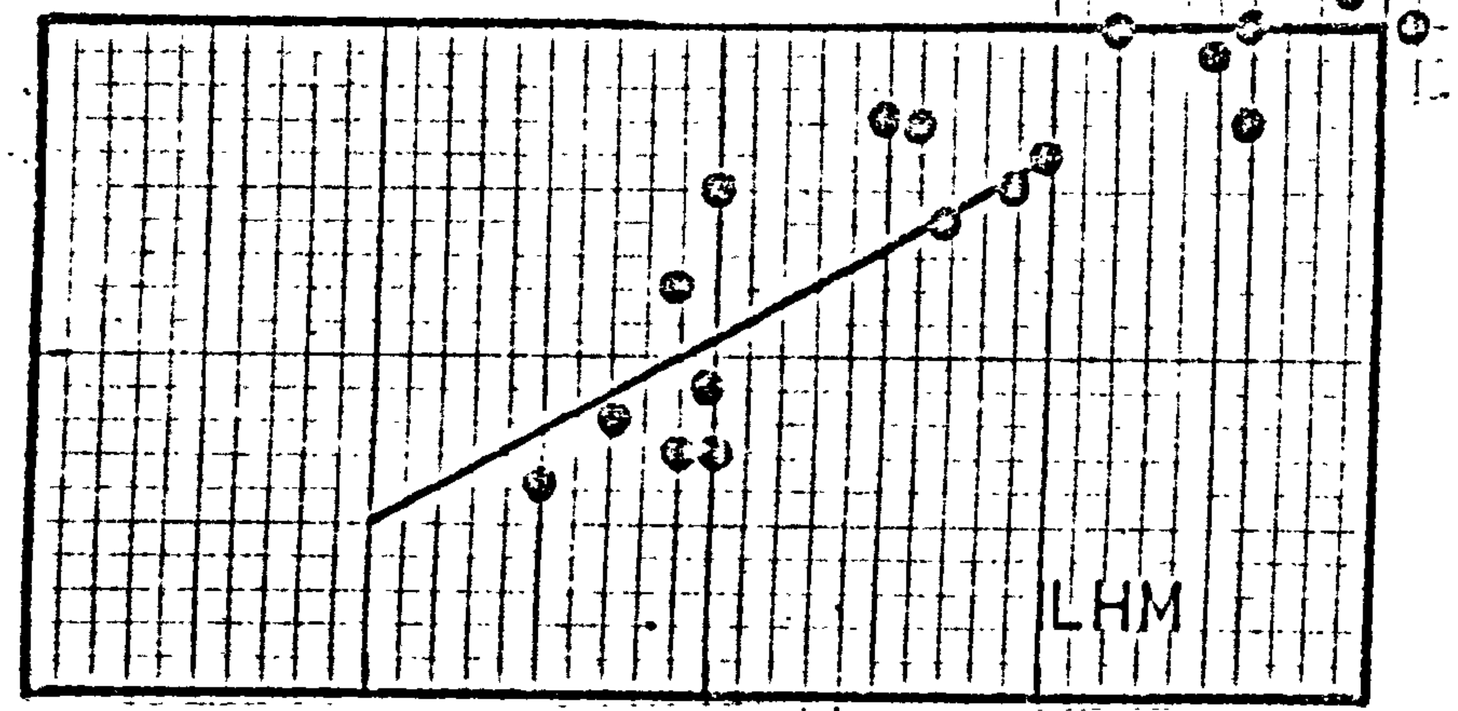
Figure 4.9 - Regression Lines. Males Eastern Brazil

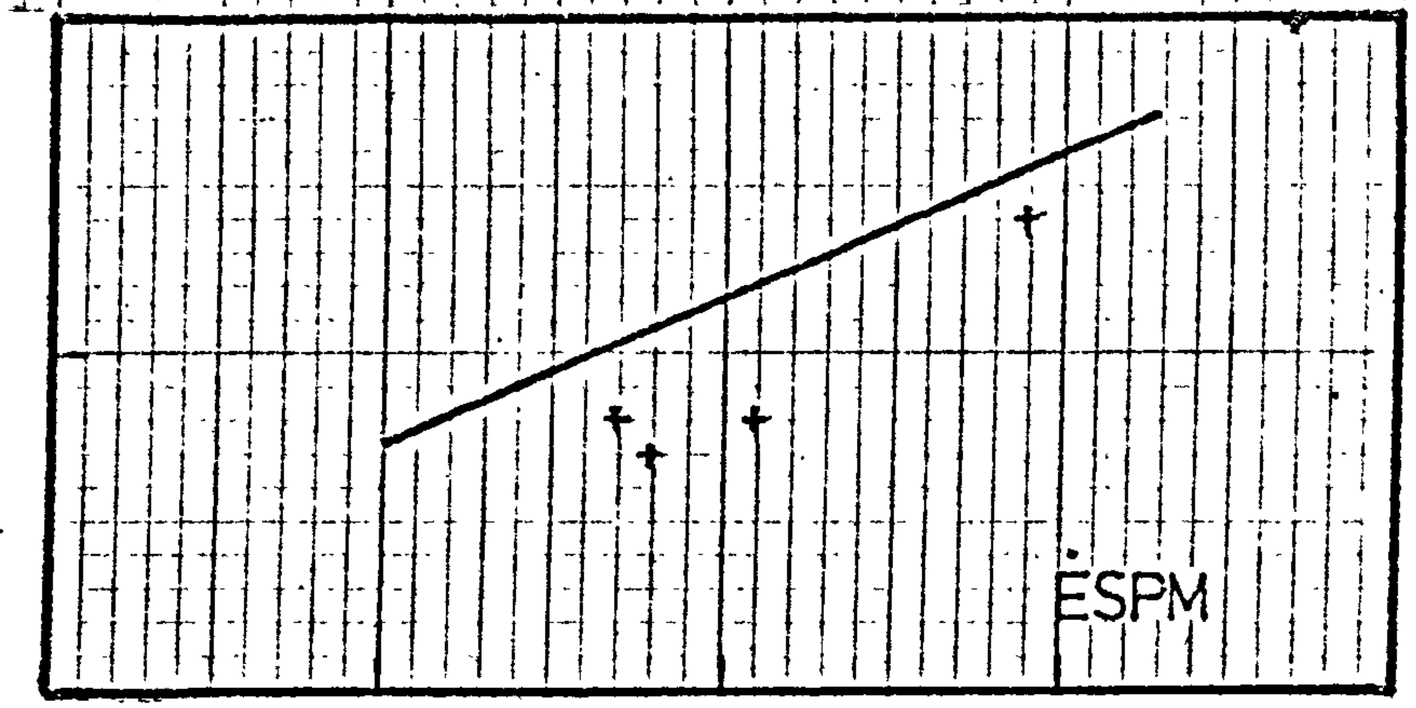
x axis = Nasal Lenght

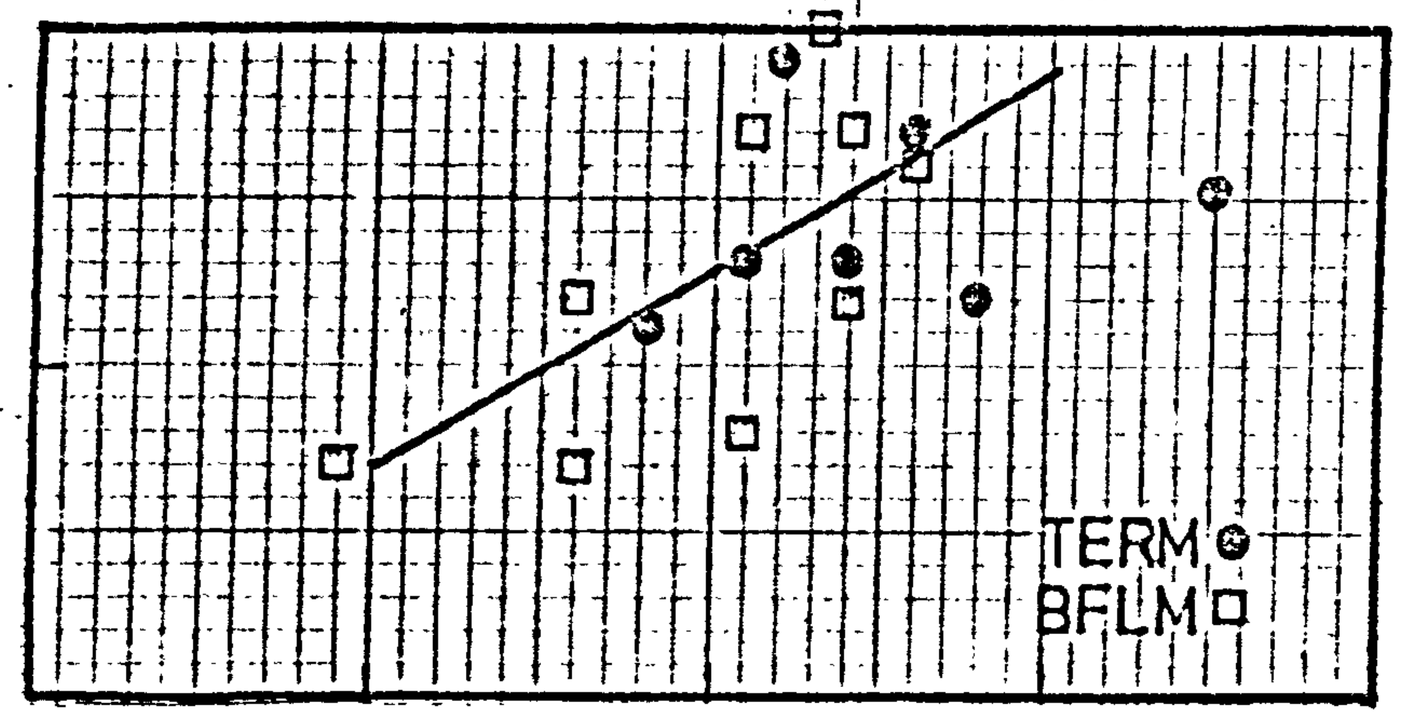
y axis = Interorbital Constriction


GBTM


26
21
16
40
45
50
55
60
COTM


LHM


ESPM


TERM
BFLM

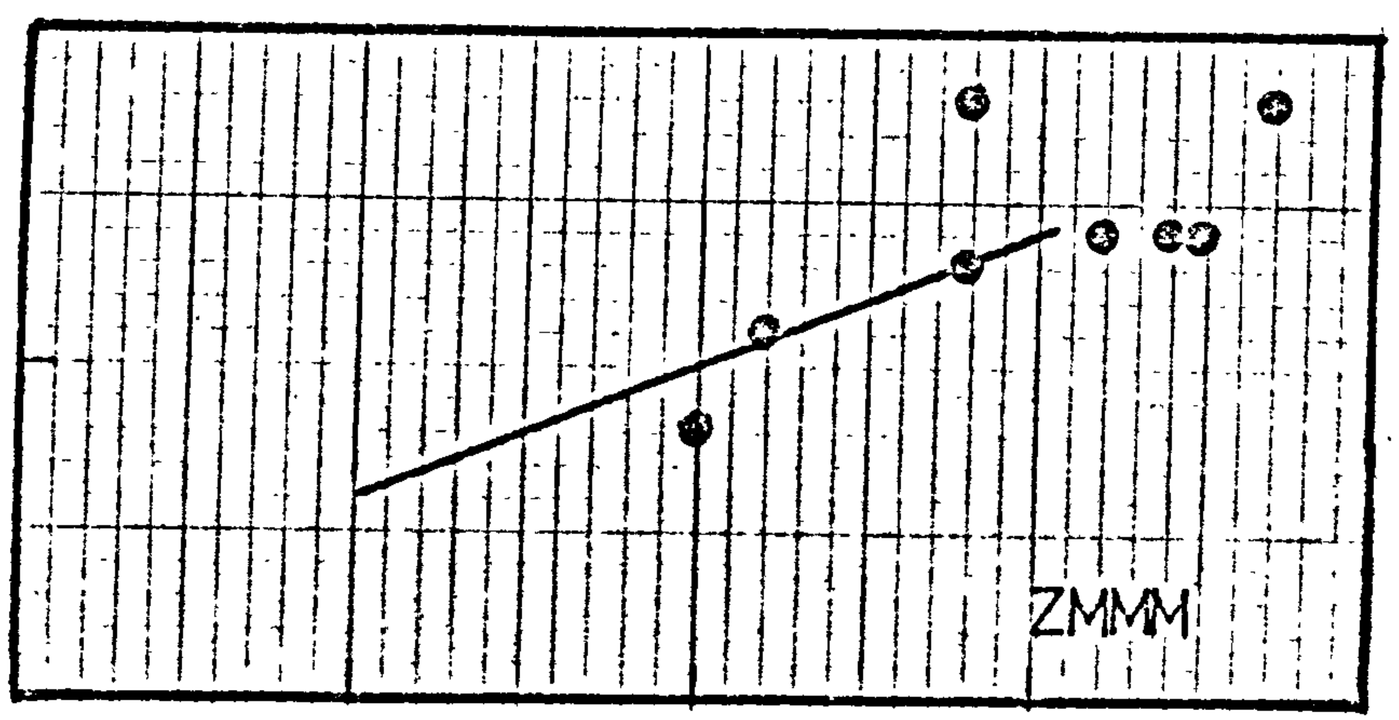

ZMMM

Table 4.3 Regression Analysis. Males Amazonia
Zygomatic bradth (Z) - Mandibular lenght (MAD)
MAD = x
Z = y

Critical value of r: * 5%

Sample	Equation	r^2	r	n_i
SENM	y = .84x - 17.85	.72	.85*	12
STMM	y = .89x - 20.82	.86	.93**	7
SURM	y = 1.13x - 38.80	.79	.89*	7

$F_{2/10} = 3.86^{*}$

Vertical bar | indicates non significant differences.

Table 4.4 Regression Analysis. Males Amazonia
Interorbital Constriction (IC) - Rostrum across Frontals (RAF)
IC = x
RAF = y

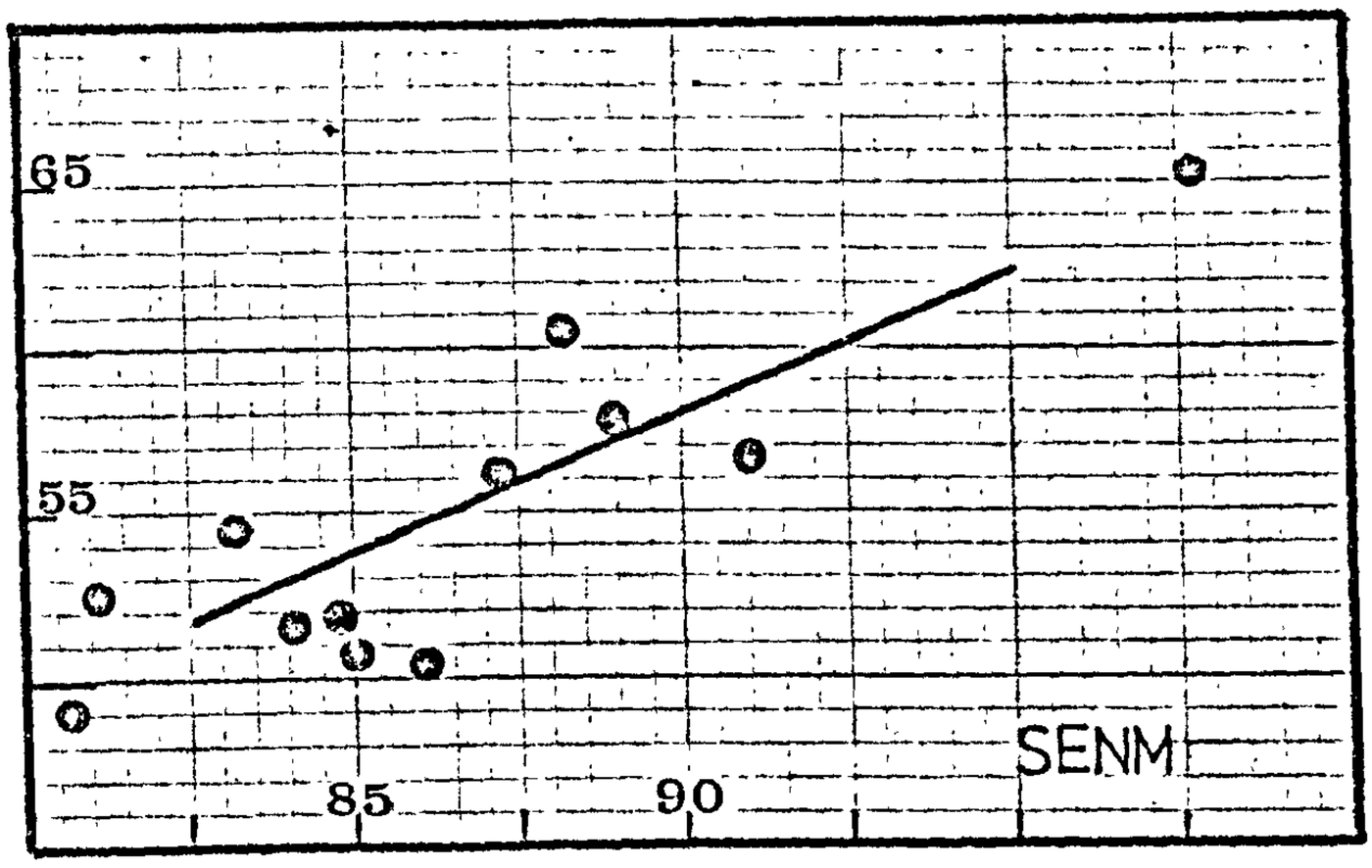
Critical value of r: ** 1%

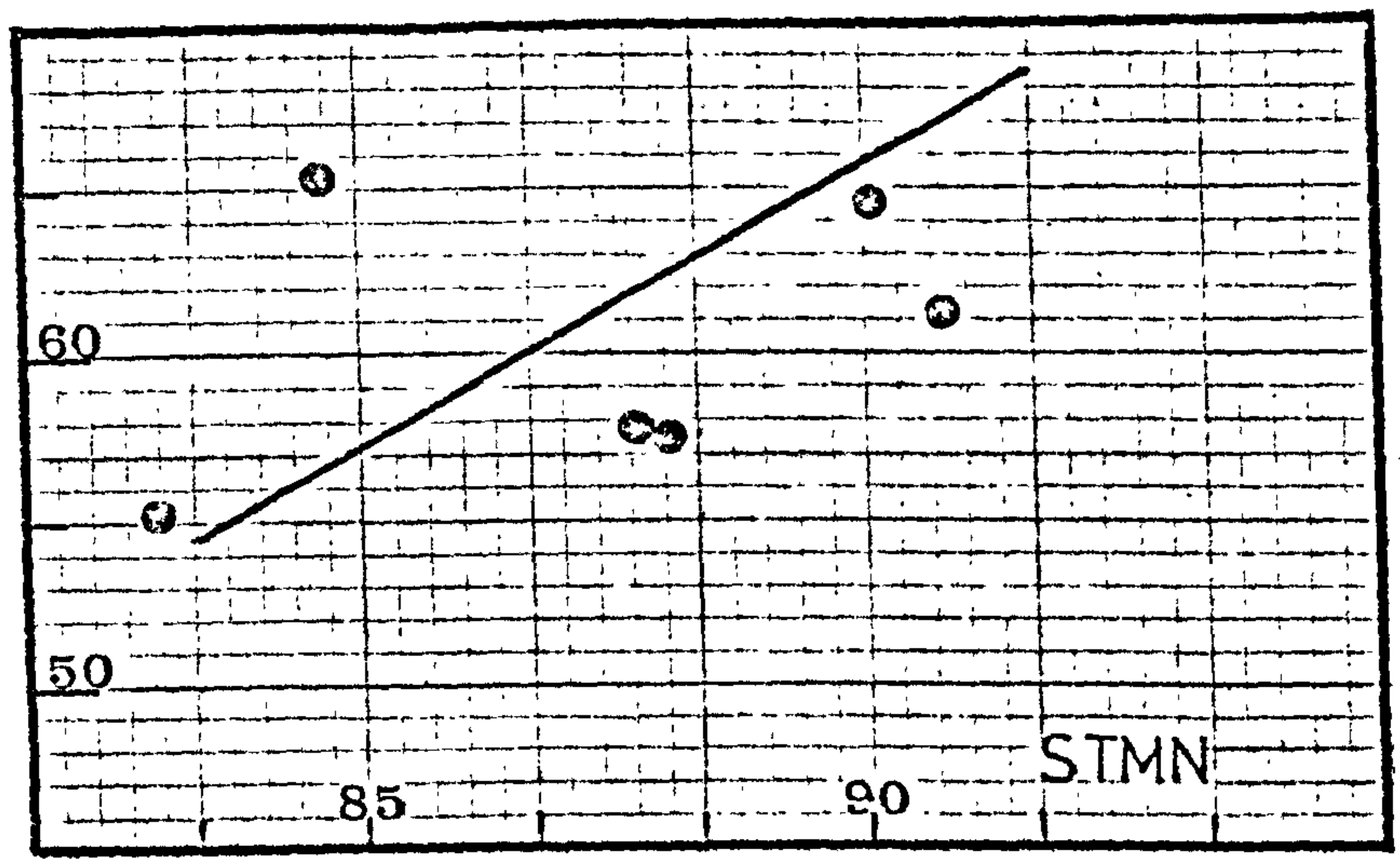
Sample	Equation	r^2	r	n_i
SENM	y = .72x + 3.06	.57	.75**	11
STMM	y = 1.07x - 4.86	.87	.93**	7
SURM	y = .62x + 4.73	.98	.95**	5
		$F_{1/17} = 1.74^{n.s.}$		
All samples	y = .85x + .04	.99	.99***	16

Table 4.5 Regression Analysis. Males Amazonia
Rostrum across Jugals (ROS) - Breadth across Canines (CAN)
ROS = x
CAN = y

Critical value of r: ** 1%

Sample	Equation	r^2	r	n
SENM	y = .88x - 5.17	.79	.84**	11
SURM	y = .71x + .09	.93	.96**	5
		$F_{1/12} = 1.09^{n.s.}$		
Both samples	y = .81x - 3.02	.82	.91**	16





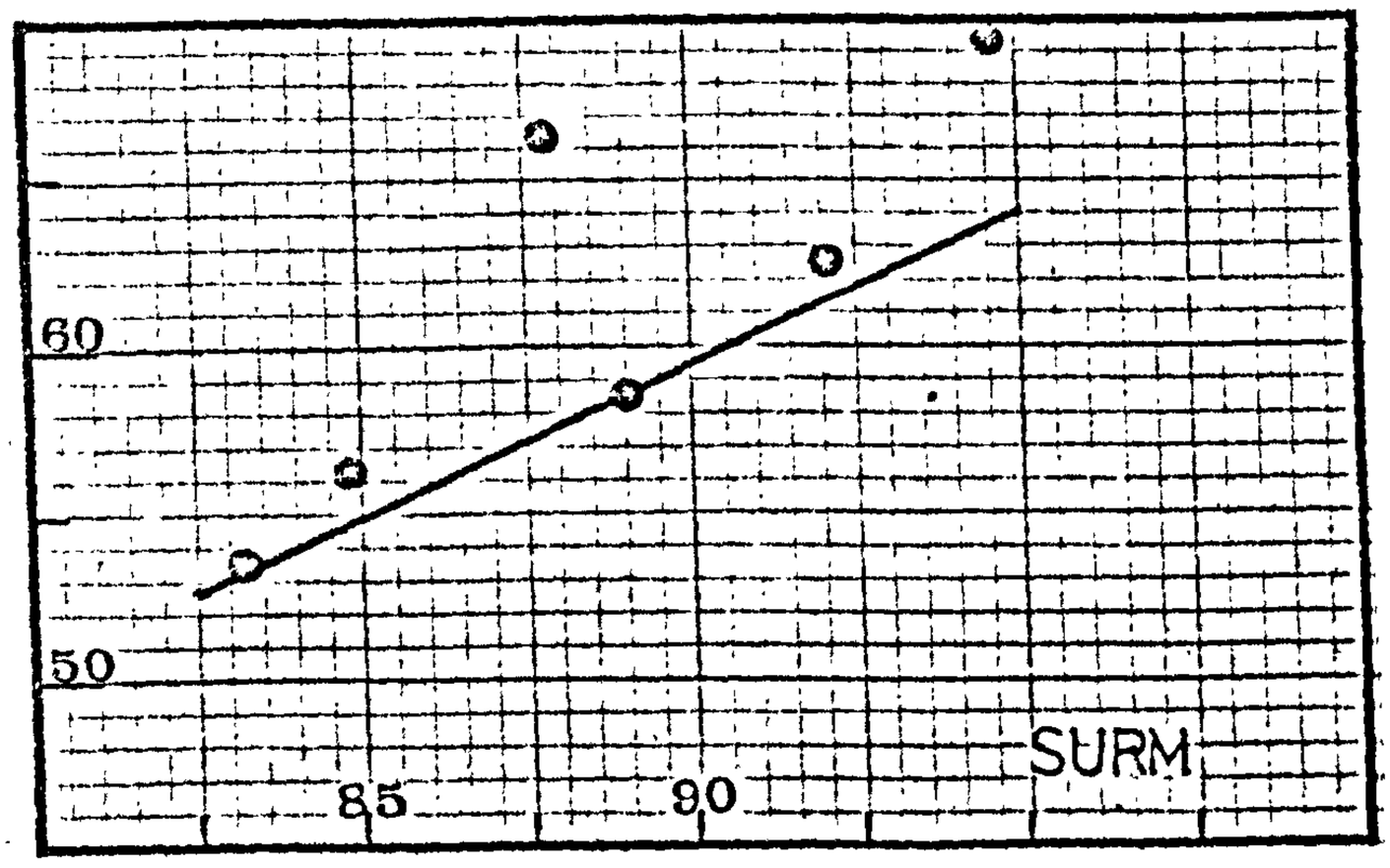
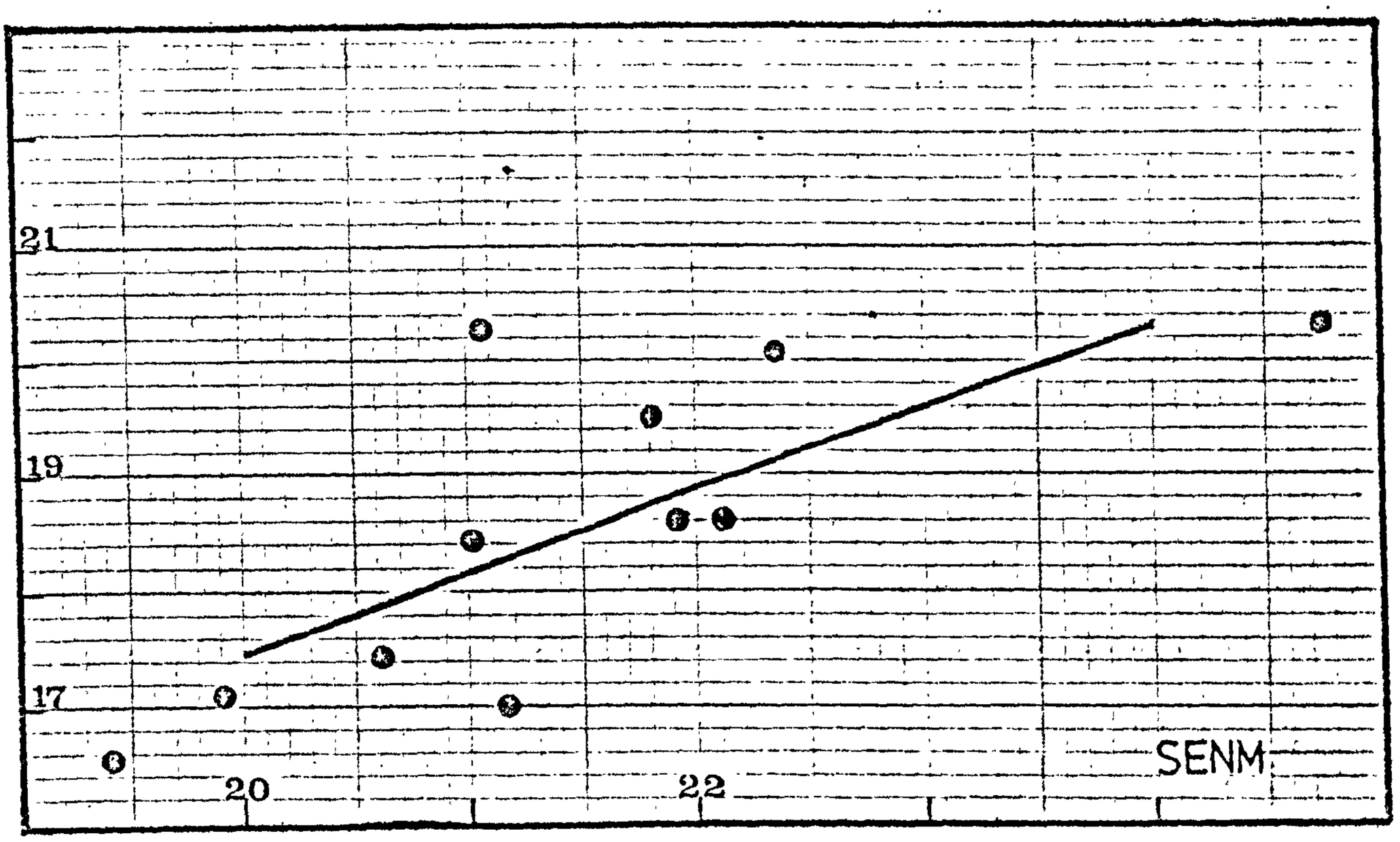


Figure 4.10 - Regression Lines. Males Northern South America

x axis = Mandibular lenght

y axis = Zygomatic breadth



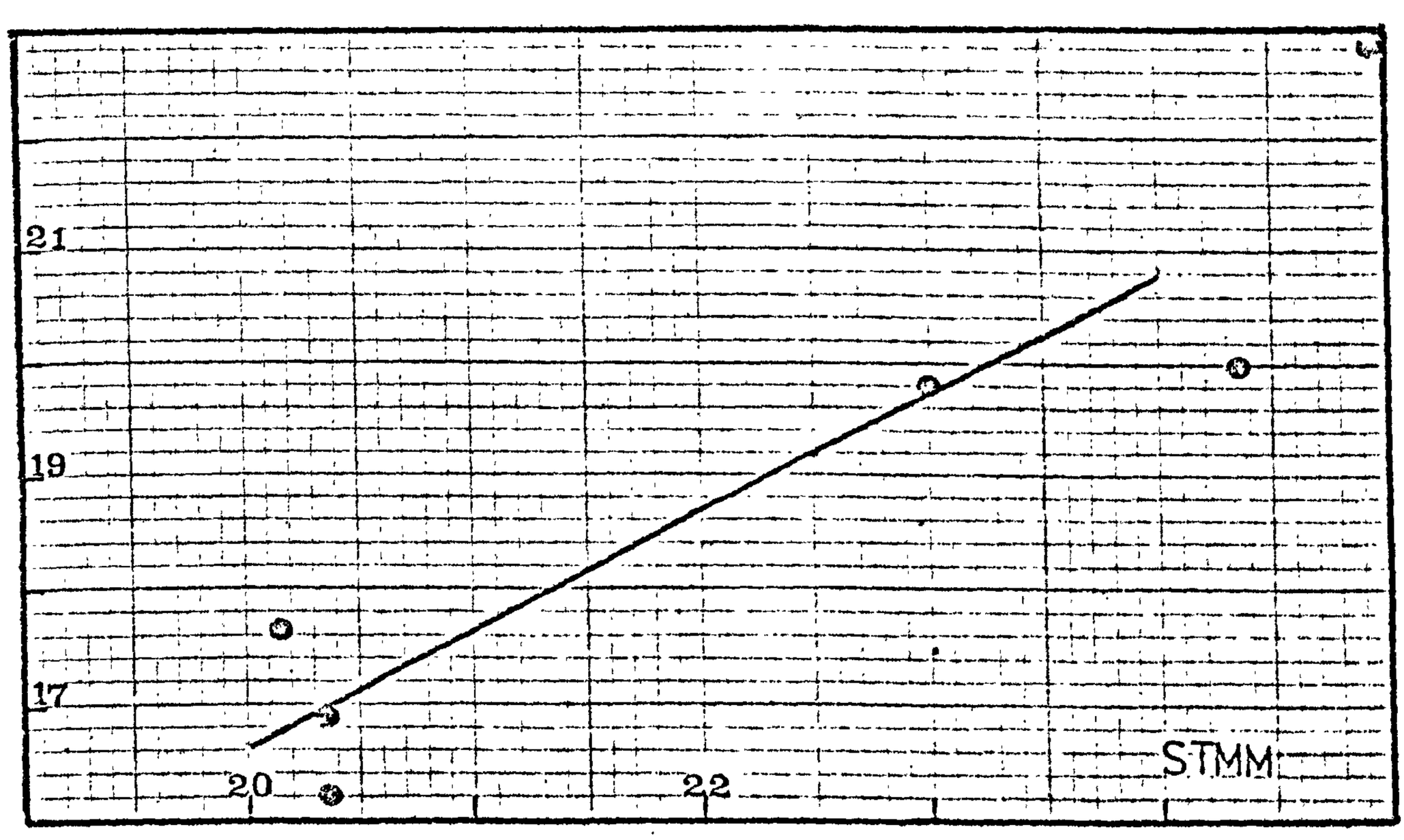


Figure 4.11 - Regression Lines. Males Northern South America.

x axis = Interorbital Constriction

y axis = Breadth of Rostrum Across Frontals

(continued)

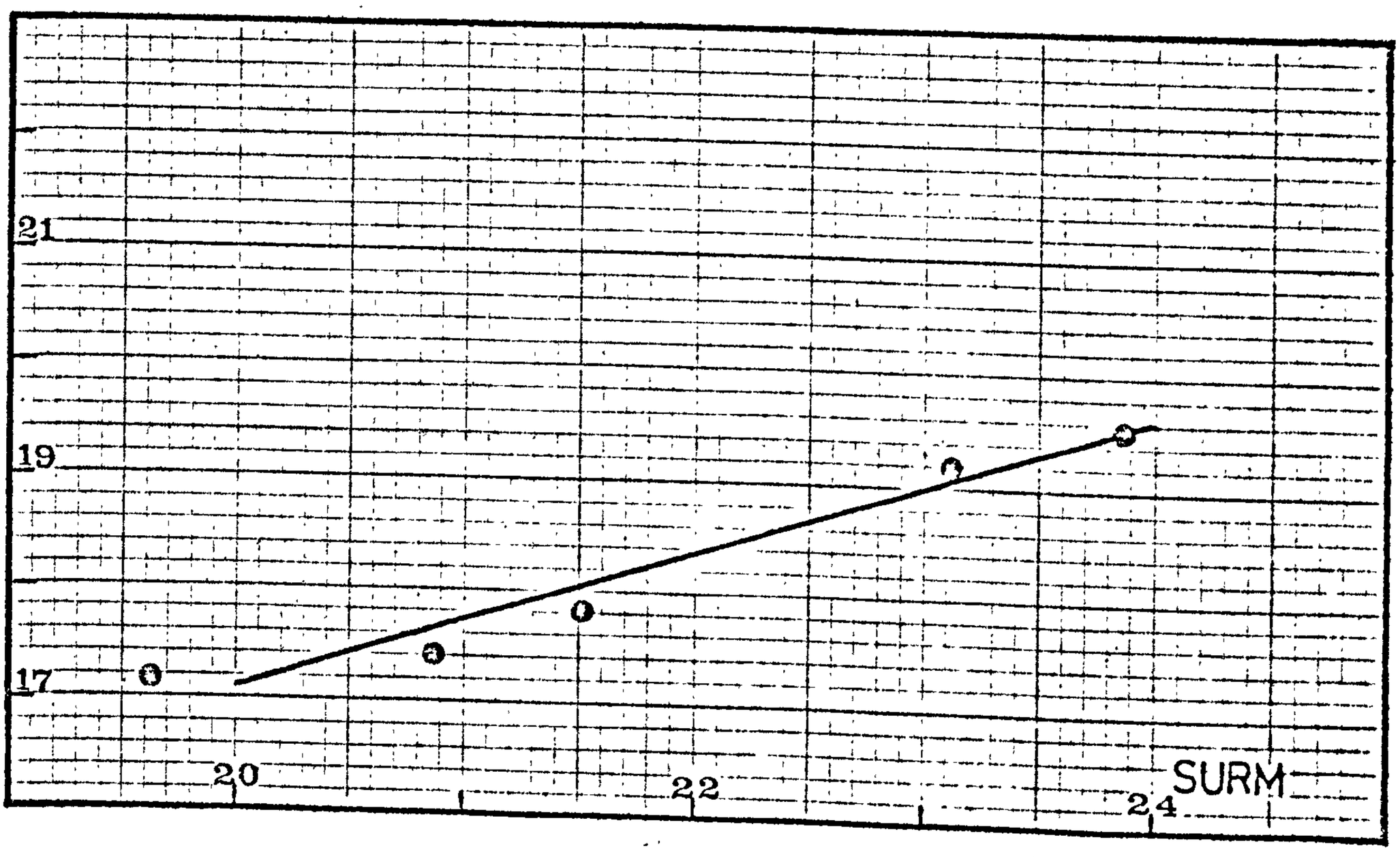
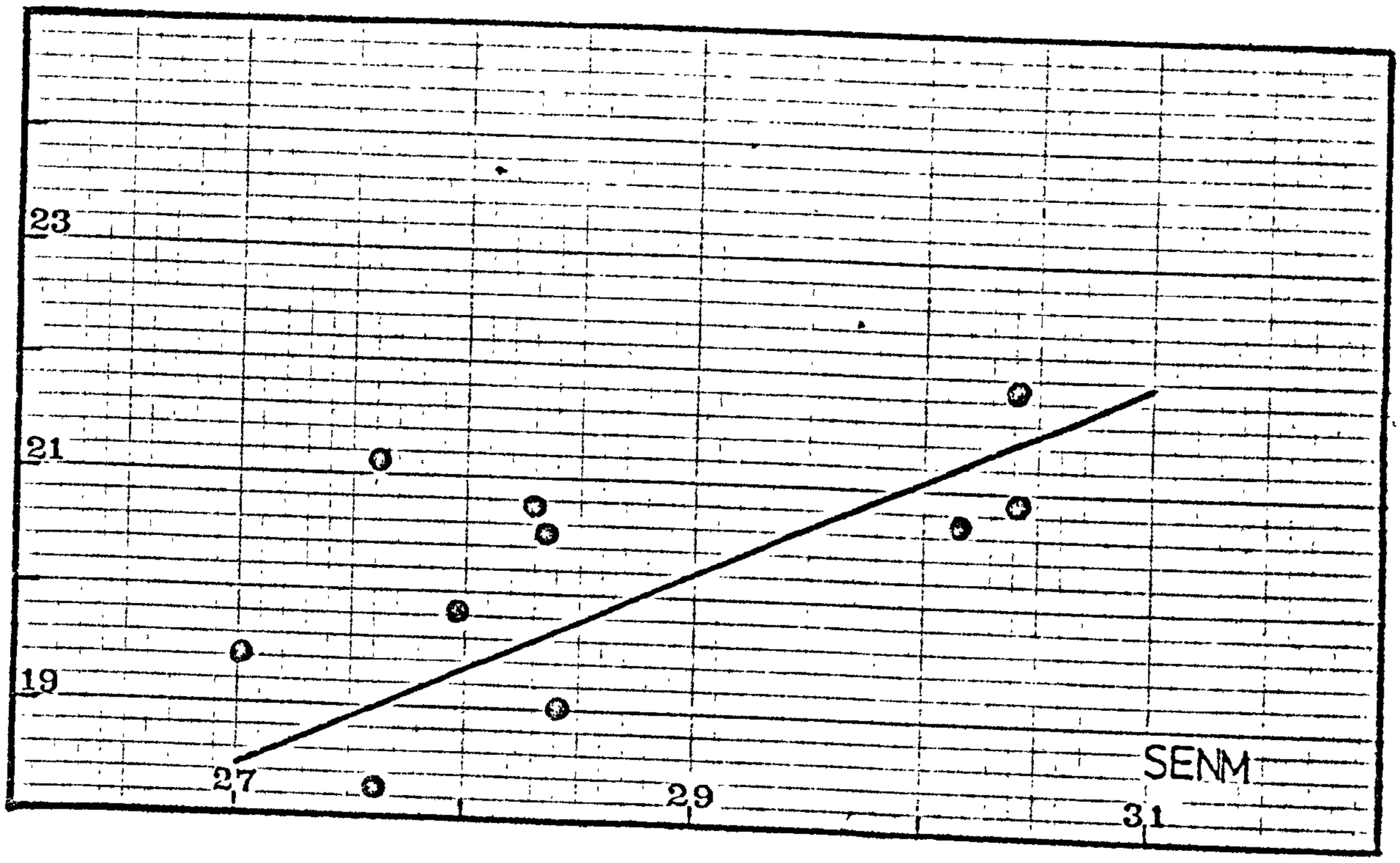


Figure 4.11 - (continuation)



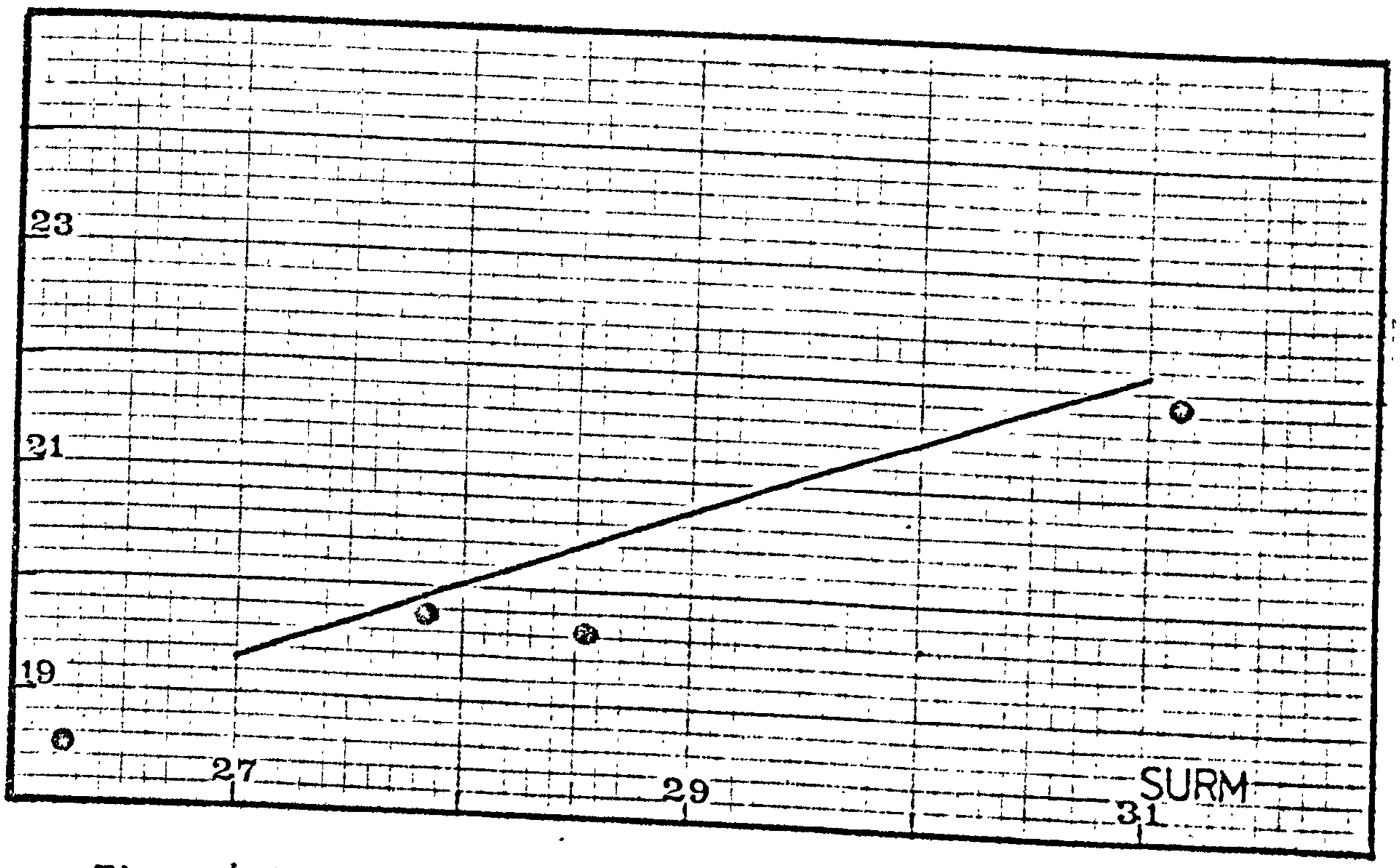


Figure 4.12 - Regression Lines. Males Northern South America.

x axis = Breadth of Rostrum Across Jugals

y axis = Breadth Across Canines

Figure 4.12 and table 4.5 show the lines and equations.

4.4.3 Northern South America: Females

As for the males, the females also had three pairs analysed. The first pair, CB and PL, was found not to be significant by the F test for all samples (Table 4.6 and figure 4.13).

The second pair, GLS and MAD, when studied gave the same negative result (Table 4.7).

The third pair has a sample in which GBN and RAF are not correlated (Surinam). The other samples have F non-significant. Table 4.8 shows the results of the analysis and figure 4.14 shows the straight line for the samples without differences.

4.5 REGRESSION ANALYSIS: DISCUSSION

The males of the Atlantic forest have a non-significant difference between the coefficients of the pair CB-Z. However for the pair NAS-IC, it seems true to say that the samples from the Zona da Mata de Minas (ZMMM), Espirito Santo (ESPM) and Ilheus (ILHM) form a group set of samples seperated from the others, which are all different the one from the other.

The results from Amazonia (since only samples from the East of Amazonia were analysed) show that in all areas considered there is no different coefficients of regression between the populations, but the Surnima samples seem to be more isolated because there is one significant difference among the males and among the females, one correlation had the r value very low for this sample. Apparently only Surinam has a greater differentiation in the form of the skull, the rest of the region having markedly similar shapes.

Table 4.6 Regression Analysis. Females Amazonia
Condylo-basal (CB) - Palatal lenght (PL)
CB = x
PL = y

Critical value of r: **1%

Sample	Equation	r^2	r	n_i
BELF	y = .67x - 4.68	.97	.99**	6
CURF	y = .45x + 16.69	.70	.84**	10
SENF	y = .44x + 18.78	.80	.89**	8
SURF	y = .57x + 4.58	.90	.95**	7
		$F_{3/23} = .55^{n.s.}$		
All samples	y = .44x + 18.55	.96	.98	31

Table 4.7 Regression Analysis. Females Amazonia
Greatest lenght of Skull (GLS) - Mandibular lenght (MAD)
GLS = x
MAD = y

Critical value of r: ** 1%

Sample	Equation	r^2	r	n_i
BELF	y = .88x - 7.13	.86	.93**	6
CALF	y = .80x + .14	.98	.99**	5
CURF	y = .69x + 13.99	.84	.91**	12
SENF	y = .51x + 31.17	.79	.89**	11
SURF	y = .89x - 8.06	.99	.99**	7
		$F_{4/31} = .75^{n.s.}$		
All samples	y = .71x + 10.55	.82	.91**	41

Table 4.8 Regression Analysis. Females Amazonia
Greatest breadth of Nasals (GBN) - Rostrum across Frontals (RAF)
RAF = x
GBN = y

Critical values of r: * 5%; ** 1%

Sample	Equation	r^2	r	n_i
BELF	y = 1.02x - 2.52	.95	.97**	6
CALF	y = .79x + .61	.73	.85*	5
CURF	y = 1.12x - 4.92	.76	.87**	13
SENF	y = .86x - .06	.72	.85**	12
SURF	y = .39x + 8.84	.32	$.56^{n.s.}$	6
All samples but SURF:		$F_{3/28} = .08^{n.s.}$		
	y = .90x - .82	.68	.82**	36

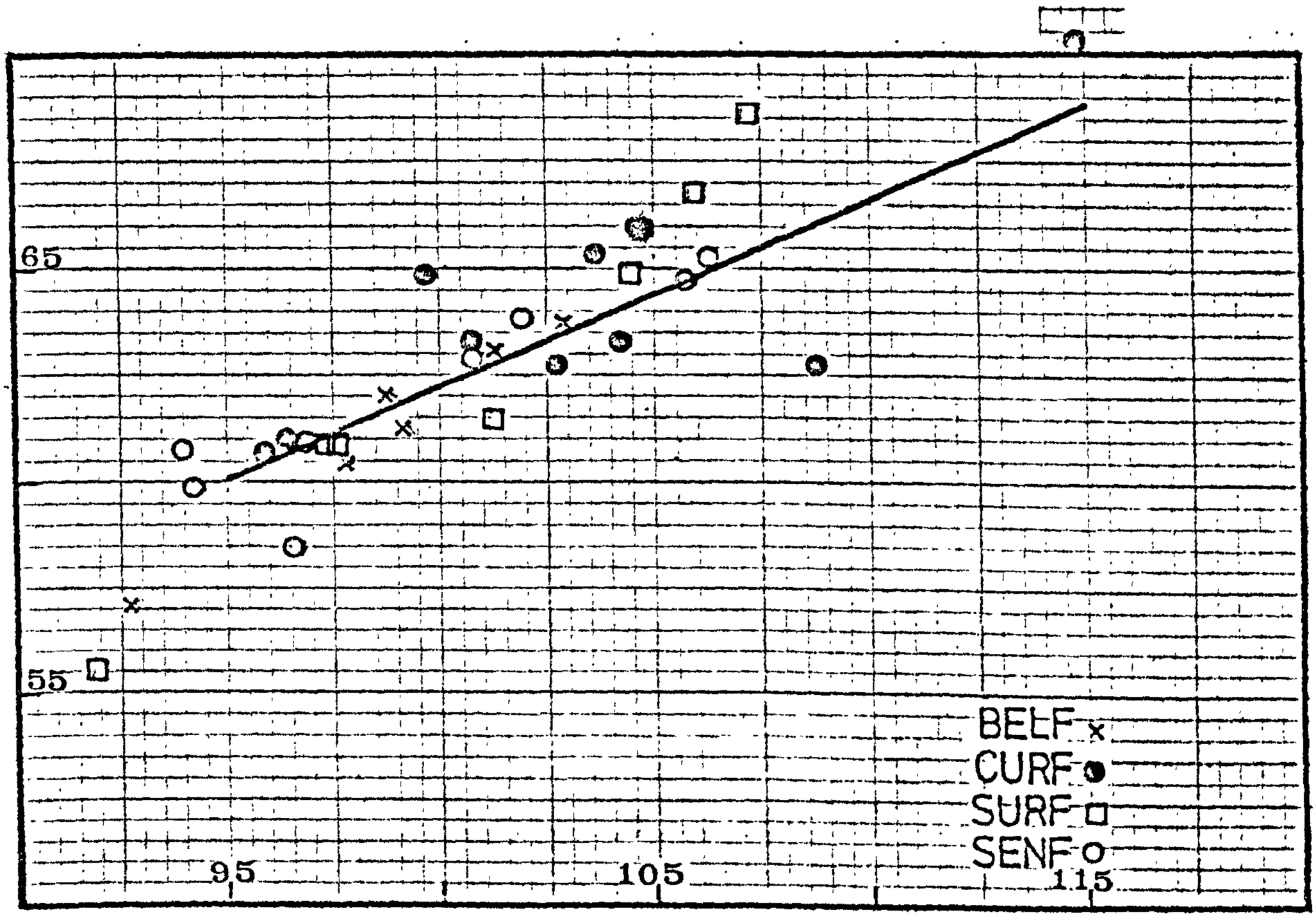


Figure 4.13 - Regression Line. Females Northern South America

x axis = Condylo-basal Lenght

y axis = Palatal Lenght

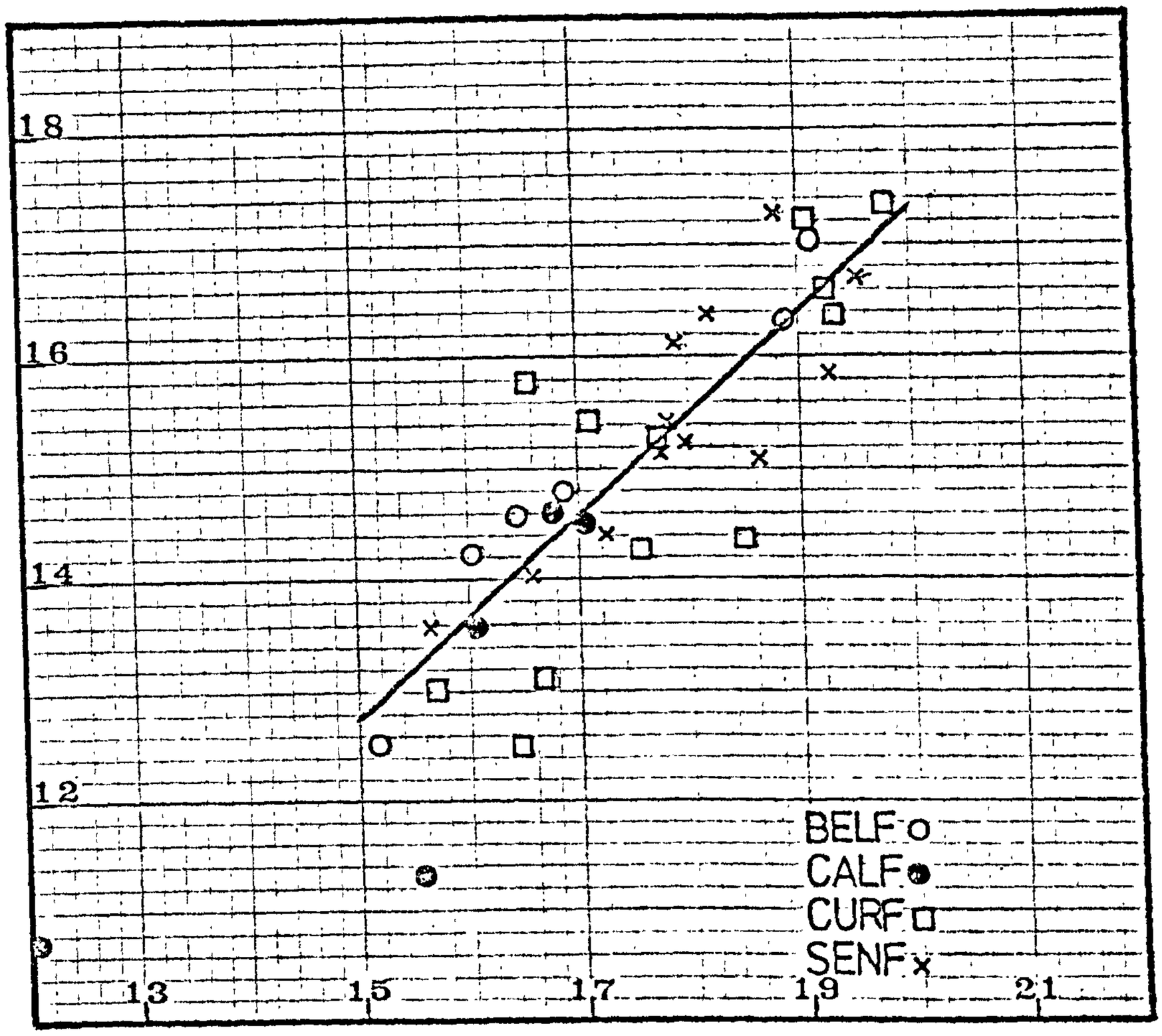


Figure 4.14 - Regression Line. Females Northern South America.

x axis = Breadth of Rostrum Across Frontals

y axis = Greatest Breadth of Nasals.

4.6 INDEPENDENT CHARACTERS: MAJOR SAMPLES

4.6.1 Eastern Brazil: Males

A Student-Newman?Keuls test was performed to see the significance of the differences among the means of the major samples Eleven characters were analysed. The results are shown in Figure 4.15, where the maximum non-significant ranges are linked by a horizontal bar. The combined percentual of non-significant results were brought together in table 4.9. From the results in this table, it can be said that Ilheus is isolated from the others as a separate set. Espirito Santo, Zona da Mata de Minas and Terezopolis have intermediate similarity with the other samples. Terezopolis, Guanabara/Tijuca and Baixada Fluminense have the highest percentuals of similarity, above 50% but this set have similarity above 30%, excepting Terezopolis, with the set Santa Catarina and Cotia.

4.6.2 Eastern Brazil: Females

Figure 4.16 and table 4.10 bring together the results of the SNK test for the major samples of females. Ilheus, Zona da Mata de Minas, Terezopolis and Baixada Fluminense have more than 60% of similarity percentual. The set above has above 30% similarity among them with Guanabara Tijuca and the Litoral of Sao Paulo. The Cotia sample shows some similarity with the Baixada Fluminense and Terezopolis. There is some sharp differences between The Baixada and Guanabara and Litoral Paulista, and between Cotia and the other samples, excepting the ones mentioned above.

Figure 4.15 - SNK Test. Major Samples. Males of Eastern Brazil.

Character	Samples							
PL	SCAM	COTM	GBTM	BFLM	TERM	ZMM	ESPM	ILHM
COP	SCAM	COTM	VAPM	GBTM	BFLM	TERM	ZMM	ILHM
CAN	SCAM	COTM	GBTM	BFLM	TERM	ZMMM	ESPM	ILHM
BAM	SCAM	COTM	GBTM	BFLM	TERM	ZMMM	ESPM	ILHM
BPS	SCAM	COTM	GBTM	BFLM	TERM	ZMMM	ILHM	
MAX	SCAM	COTM	BFLM	GBTM	TERM	ZMMM	ESPM	ILHM
SM	SCAM	COTM	GBTM	TERM	ZMMM	ESPM	ILHM	
ROS	SCAM	COTM	GBTM	BFLM	TERM	ZMMM	ESPM	ILHM
GBN	SCAM	COTM	GBTM	BFLM	TERM	ZMMM	ESPM	ILHM
RAF	SCAM	COTM	GBTM	BFLM	TERM	ZMMM	ESPM	ILHM
MAD	SCAM	COTM	VAPM	GBTM	BFLM	TERM	ZMMM	ESPM	ILHM
SIM	SCAM	COTM	GBTM	BFLM	TERM	ZMMM	ESPM	ILHM

Figure 4.16 - SNK Test. Major Samples. Females of Eastern Brazil.

Character Samples.

CB	COTF	LITF	GBTF	BFLF	TERF	ZMMF	ILHF
PL	COTF	LITF	GBTF	BFLF	TERF	ZMMF	ILHF
Z	COTF	LITF	GBTF	BFLF	TERF	ZMMF	ILHF
IC	COTF	LITF	GBTF	BFLF	TERF	ZMMF	ILHF
COP	COTF	LITF	GBTF	BFLF	TERF	ZMMF	ILHF
CAN	COTF	LITF	GBTF	BFLF	TERF	ZMMF	ILHF
BAN	COTF	LITF	GBTF	BFLF	TERF	ZMMF	ILHF
BPS	COTF	LITF	GBTF	BFLF	TERF	ZMMF	ILHF
MAX	COTF	LITF	GBTF	BFLF	TERF	ZMMF	ILHF
SM	COTF	LITF	GBTF	BFLF	TERF	ZMMF	ILHF
ROS	COTF	LITF	GBTT	BFLF	TERF	ZMMF	ILHF
RAF	COTF	LITF	GBTF	BFLF	TERF	ZMMF	ILHF
SIM	COTF	LITF	GBTF	BFLF	TERF	ZMMF	ILHF

Table 4.9 - Percentage of Non Significant Differences Between Samples of Males in Eastern Brazil. SNK Test.

	SCAM	COTM	GBTM	BFLM	TERM	ZHMM	ESPM	ILHM
SCAM	-							
COTM	36	-						
GBTM	36	36	-					
BFLM	33	30	50	-				
TERM	27	27	56	56	-			
ZHMM	10	9	36	22	42	-		
ESPM	0	0	0	29	38	33	-	
ILHM	9	9	9	0	9	27	13	-

Table 4.10 - Percentage of Non Significant Differences Between Samples of Females in Eastern Brazil. SNK Test.

	COTF	LITF	GBTF	BFLF	TERF	ZHMF	ILHF
COTF	-						
LITF	15	-					
GBTF	15	31	-				
BFLF	38	15	23	-			
TERF	38	31	31	62	-		
ZHMF	15	31	31	31	62	-	
ILHF	15	31	38	38	62	62	-

4.6.3 Northern South America: Males

Only three samples of males in Amazonia were suitable for analysis. From figure 4.17 and table 4.11 it can be seen, very clearly, that the Serra do Navio sample is isolated from the others with a very low percentage of similarity. On the other hand, Santarem has an above 90% similarity to Surinam.

4.6.4 Northern South America: Females

The pattern for females in Amazonia and the Pacific Forest is complicated. An odd set of similarities is found between all samples and that of the Cauca Valley, one which is several times more similar than that with the neighbours. Belem, Caldeirao and Curralinho have above 50% similarities. Serra do Navio and Surinam have a 50% similarity with Santarem. But Surinam only has 45% with Serra do Navio. Belem is less similar to any samples other than the ones mentioned above. And even when seperated from Belem, Serra do Navio and Santarem are quite similar, for the levels present, to Curralinho and Caldeirao.

4.7 INDEPENDENT CHARACTERS: MAJOR SAMPLES: DISCUSSION

4.7.1 Eastern Brazil

With a similarity of the percentual being less than 30%, it can be seen that a stepped difference occurs between Ilheus and all the other samples among males. However, the same does not occur among females, but the Zona da Mata and Terezopolis have a high degree of similarity with Ilheus. Espirito Santo can be considered similar with Ilheus as well. For most of the samples it is difficult to compare males with females, not only because

Figure 4.17 - SNK Test.Southern South America. Major Samples. Males.

Characters	Samples		
GLS	SENM	SURM	STRM
PL	SENM	SURM	STRM
COP	SENM	SURM	STRM
BAM	SENM	SURM	STRM
BBC	SENM	SURM	STRM
BPS	SENM	SURM	STRM
MAX	SENM	SURM	STRM
SM	SENM	SURM	STRM
GBN	SENM	SURM	STRM
NAS	SENM	SURM	STRM
SIM	SENM	SURM	STRM

Figure 4.18 - SNK Test.Northern South America.Major Samples.Females.

Characters . . Samples

Z BELF CURF CALF SENF SURF

IC BELF CURF SENF SURF STMF

COP BELF CALF CAUF CURF SENF SURF STMF

CAN BELF CALF CURF SENF SURF CAUF

BBC BELF CALF CURF SENF SURF STMF CAUF

BPS BELF CURF SENF SURF STMF CAUF

MAX BELF CALF CURF SENF SURF STMF CAUF

SM BELF CALF CURF SENF SURF STMF CAUF

ROS BELF CURF SENF SURF CAUF

NAS CURF SENF SURF STMF CAUF

STH BELF CALF CURF SENF SURF STMF CAUF

Table 4.11 - Percentage of Non Significant Differences between Samples of Males in Northern South America. SNK Test.

	SENM	SURM	STMM
SENM	-		
SURM	27	-	
STMM	18	91	-

Table 4.12 - Percentage of Non Significant differences between Samples of Females in Northern South America. SNK Test.

	BELF	CALF	CURF	SENF	SURF	STMF	CAUF
BELF	-						
CALF	57	-					
CURF	60	71	-				
SENF	20	43	64	-			
SURF	10	29	36	45	-		
STMF	14	50	63	50	50	-	
CAUF	63	83	89	56	33	43	-

they do not have the same samples, but because it is not expected that both sexes have to have the same pattern. Abstracting these differences, the analysis of the results suggests a pattern for the males where Ilheus is differentiated from the other samples; Espirito Santo, Zona da Mata and Terezopolis form the second set; the third set being composed by Santa Catarina, Cotia, Guanabara and Baixada Fluminence. However, the latter with Terezopolis and Guanabara are a very similar fourth set. Apparently, the Serra do Mar acts as a barrier of some sort, but no likely barrier exists between Ilheus and the others.

The females do not show the isolation of Ilheus, which forms a clear set with the Zona da Mata and Terezopolis. These latter two have a link with Baixada Fluminense. itoral de Sao Paulo and Guanabara form a second set. A stepped difference exists between this set and Cotia as well as with the Baixada. Here, the Serra do Mar does not seem to be the barrier, but the litoral samples are clearly differentiated from the hinterland ones. Cotia has approximately the same degree of similarity with the other Serra do Mar sample (Terezopolis) and the Baixada as the litoral ones have between them.

The combined picture of both males and females, leaving aside the Serra do Mar samples (Terezopolis and Cotia), as well as the Baixada Fluminense, suggests that from the Vale to Paraiba, leeward of Serra do Mar to the North, there is a set of populations and windward the Serra, in the littoral, another one. The somewhat confused picture of the Baixada and Terezopolis now linked with the litoral, now with the Vale do Paraiba, the Baixada, sometimes more similar to Guanabara, sometimes to Terezopolis, is due to the

fact that this is an intermediate zone of intergradation, a "hybrid" zone. Later, the details and explanation will be discussed, following an analysis of the transects.

4.8 THE TRANSECTS

4.8.1 Eastern Brazil: Males

1. Palatal Length.

a. Coastal Transect - There is one break (at 5% level, here and in the rest of this paper) between Ilheus and Espirito Santo. Sao Miguel, Alagoas, is quite the same population as Ilheus. The probabilities between Guanabara and the populations at the north up to Espirito Santo are very high. Between Guanabara and the southern littoral these are lower than up to the north. There is another break between Guanabara and the Baixada. However, the links between the former and the other populations north and south, show a pattern in all similar to Guanabara. Santa Catarina and Bananal have a probability lower than the 90% level, the former being quite linked with the other in the southern littoral.

b. Ilheus-Bananal transect - Again there is the same break between Ilheus and Espirito Santo. The latter has non-significant differences with Zona da Mata. Zona da Mata and Sao Joao Marcos, in the Serra do Mar, have a low probability, but going south through the Paraiba Valley, the neighbouring populations of Zona da Mata and Cotia have very low probability. The same applies to Cotia and Bananal.

c. Litoral-Lins - This transect shows no breaks. Campinas and Cotia have a smaller probability but the localities further west

TABLE 4.13 PALATAL LENGHT EASTERN BRAZIL MALES BASIC STATISTICS

SAMP	N	MEAN	SDEV	SERR	CV	RANGE		AVSDEV		CONFL	
COTM	15	60.07	3.23	0.86	5.53	55.20	69.90	56.84	63.30	58.23	61.89
SCAM	6	64.17	4.14	1.69	6.45	58.60	70.65	60.03	68.31	59.83	68.51
GBTM	6	62.26	2.64	1.08	4.25	58.65	65.70	59.62	64.90	59.62	64.90
TERM	8	61.66	2.91	1.03	4.73	55.50	63.95	58.75	64.57	59.28	64.03
IMMM	10	62.92	3.49	1.10	5.55	56.85	66.90	59.43	64.41	60.46	65.38
ILHM	18	64.79	3.59	0.85	5.55	58.30	69.65	61.20	68.38	63.11	66.57
BFLM	5	61.57	1.89	0.84	3.07	59.60	64.65	59.68	63.46	59.40	63.64
BANM	4	63.24	0.00	0.00	0.00	59.85	64.80	0.00	0.00	0.00	0.00
LITM	2	56.75	0.00	0.00	0.00	55.70	57.60	0.00	0.00	0.00	0.00
CAPM	1	69.90	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
LINM	1	69.75	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
SFXM	1	58.90	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
ITUM	3	61.33	0.00	0.00	0.00	59.50	63.50	0.00	0.00	0.00	0.00
VAPM	4	60.65	0.00	0.00	0.00	58.50	62.40	0.00	0.00	0.00	0.00
SJMM	1	70.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
MNGM	2	62.05	0.00	0.00	0.00	61.00	63.10	0.00	0.00	0.00	0.00
SMAM	1	61.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
ESPM	6	63.23	4.55	1.86	7.20	57.55	69.10	58.68	67.78	58.46	68.01
SMGM	1	61.60	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Table 4.14 - Males of Eastern Brazil. Levels of Probability of Significant Differences Between Samples. **Palatal Lenght**

Sample	p	SNK	
Coastal Transect			
Smgm/ILHM	.9		
ILHM/ESPM		*	break
ESPM/Smam	.8		
Smam/GBTM	.7		
GBTM/Mngm	.4		
GBTM/Litm	.2		
GBTM/Banm	.6		
GBTM/SCAM		*	break
Smam/BFLM	.7		
BFLM	.7		
BFLM/Litm	.2		
BFLM/Banm	.9		
BFLM/SCAM		*	break
SCAM/Banm	.9		
SCAM/Litm	.6		
SCAM/Ilngm	.9		
Ilheus-Bananal Transect			
ESPM/ZMTM		*	break
ZMTM/Sjmm	.2		
ZMTM/Vapm	.9		
Vapm/COTM	.9		
COTM/Banm	.9		
Litoral-Lins Transect			
Litm/COTM	.9		
COTM/Capm	.3		
COTM/Linm	.4		
Santa Catarina-Lins Transect			
SCAM/Banm	.9		
SCAM/Linm	.8		

have lower probabilities.

d. Santa Catarina-Lins - Very low probabilities between Santa Catarina and localities to the west.

e. Summary - Ilheus and Sao Miguel are clearly separated from the other populations further South. Intergradation occurs in all populations which are intermediate between the major samples. Localities north and south of Guanabara and Baixada may belong to one or another population. The value of the probabilities, indicated that some difference occurs between these localities and the southern littoral ones. Apparently the parameters are the same on both sides of the Serra do Mar and further west.

2. Postorbital Constriction (Table 4.15)

a. Coastal Transect - Again, Ilheus and Sao Miguel are isolated. There is a break between Espirito Santo and localities south. These breaks will occur in all comparisons made along the transect to the South.

b. Ilheus-Bananal Transect - Excepting the test between Sao Joao Marcos and the Zona da Mata, all comparisons were found significant.

c. Litoral-Lins Transect - Only the test between Cotia and Ituverava was found not significant.

d. Guanabara-Lins Transect - Terezopolis and Sao Joao Marcos are non-significant. The former have a break with Zona da Mata, this one with lower probabilities further west.

TABLE 4.15 POSTORBITAL EASTERN BRAZIL MALES BASIC STATISTICS

SAMP	N	MEAN	SDEV	SERR	CV	RANGE		AVSDEV		CONFL	
SCAM	7	11.37	0.29	0.11	2.57	11.00	11.70	11.08	11.66	11.10	11.64
COTM	17	11.37	0.46	0.11	4.05	10.60	12.15	10.91	11.83	11.13	11.61
GOTM	7	11.06	0.47	0.18	4.29	10.25	11.65	10.59	11.53	10.64	11.49
TERM	11	11.32	0.45	0.14	4.00	10.70	12.20	10.87	11.77	11.02	11.65
ZMMM	10	11.26	0.45	0.14	4.01	10.75	11.95	10.81	11.71	10.95	11.58
ILHM	18	11.40	0.57	0.14	5.23	10.35	12.15	10.83	11.97	11.12	11.68
BFLM	7	11.57	0.43	0.16	3.70	11.15	12.20	11.14	12.00	11.19	11.95
BANM	4	11.38	0.00	0.00	0.00	11.20	11.65	0.00	0.00	0.00	0.00
LITM	3	11.37	0.00	0.00	0.00	10.70	11.90	0.00	0.00	0.00	0.00
CAPM	1	10.60	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
LINM	1	11.45	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
SFXM	1	11.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
ITUM	3	11.80	0.00	0.00	0.00	11.15	12.40	0.00	0.00	0.00	0.00
VAPM	5	10.98	0.37	0.17	3.37	10.60	11.60	10.61	11.35	10.52	11.44
SJMM	1	11.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
MNGM	2	11.08	0.00	0.00	0.00	10.75	11.40	0.00	0.00	0.00	0.00
SMAM	1	12.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
PDCM	1	11.45	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
ESPM	6	11.10	0.44	0.18	3.97	10.50	11.75	10.66	11.54	10.64	11.56
SMGM	1	11.75	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
PDC	1	61.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Table 4.16 - Males of Eastern Brazil. Levels of Probabilty of Significant Differences Between Samples. Postorbital.

Sample	p	SNK	
Coastal Transect			
Smgm/ILHM	.2		
ILHM/ESPM		*	break
ESPM/Smam	.01	**	break
Smam/GBTM	.001	***	break
GBTM/ Mngm	.01	**	break
Smam/BFLM	.05	*	break
BFLM/Mngm	.01	*	break
SCAM/Banm	.001	***	break
Ilheus-Bananal Transect			
ESPM/ZMMM		*	break
ZMMM/Sjmm	.5		
ZMMM/VAPM		*	break
VAPM/COTM		*	break
COTM/Banm	.001	***	break
Litoral-Lins Transect			
Litm/COTM	.001	***	break
COTM/Capm	.001	***	break
COTM/Pdcm	.001	***	break
COTM/Itum	.5		
COTM/Linm	.001	***	break
Floresta da Tijuca-Lins Transect			
GBTM/BFLM		*	break
BFLM/TERM		*	break
TERM/Sjmm	.5		
TERM/ZMMM		*	break
ZMMM/Pdcm	.4		
ZMMM/Itum	.1		
ZMMM/Linm	.4		
Santa Catarina-Lins Transect			
SCAM/Banm	.001	***	break

e. Santa Catarina-Lins Transect - Being that Bananal and Santa Catarina are different, the analysis was stopped.

f. Summary - This character can be considered a distributed mosaic. However, the two populations form Serra da Mar, being near, and are not significant. The same applies for all population west when compared with Zona da Mata.

3. Breadth across (Anines Table 4.17)

a. Coastal Transect - The populations of the Northeast, Ilheus and Sao Miguel belong to the same set and there is a break with the populations further South.

There is no gap between the Macae sample and Guanabara. However, this sample seems nearer to Guanabara than to the Baixada and Espirito Santo. A similar pattern exists between the Baixada and the Mangaratiba Litoral, and between the latter and Guanabara. Mangaratiba litoral and Bananal form a set well related with Guanab ara and Santa Catarina.

b. Ilheus-Bananal Transect - The Espirito Santo has a significant difference with the Zona da Mata. This locality is linked with Sao Joao Marcos, but a clinal variation appears to exist between it and Cotia, the two extremes being significantly different. Cotia and Bananal belong to the same set.

c. Litoral-Lins Transect - Litoral, Cotia, Pocos de Calda and Ituverava and Lins do not show differentiation. However, the pattern of this transect does not seem to be clinal, long distance localities bearing more similarity than near one. Campinas, a single

TABLE 4.17 ACROSS CANINES EASTERN BRAZIL MALES BASIC STATISTICS

SAMP	N	MEAN	SDEV	SERR	CV	RANGE		AVSDEV		CONFL	
SCAM	5	20.42	2.60	1.16	12.75	18.05	24.10	17.82	23.02	17.19	23.65
COTM	17	18.71	1.91	0.46	10.18	16.05	23.30	16.80	20.62	17.74	19.69
GBTM	7	20.21	2.38	0.90	11.76	17.50	23.55	17.83	22.59	18.08	22.33
TERM	7	19.02	1.27	0.48	10.89	17.60	21.00	17.75	20.29	17.89	20.15
ZMMM	10	20.38	1.45	0.46	7.12	18.05	22.35	18.93	21.83	19.36	21.40
ILHM	11	21.36	1.96	0.59	9.17	18.15	23.55	19.40	23.32	20.06	22.66
BFLM	7	20.45	1.25	0.47	6.12	18.60	21.85	19.20	21.70	19.33	21.57
BANM	3	19.97	0.00	0.00	0.00	19.60	20.25	0.00	0.00	0.00	0.00
LITM	2	18.53	0.00	0.00	0.00	18.20	18.85	0.00	0.00	0.00	0.00
CAPM	1	23.30	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
LINM	1	22.75	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
ITUM	3	19.67	0.00	0.00	0.00	19.40	19.90	0.00	0.00	0.00	0.00
VAPM	3	18.80	0.00	0.00	0.00	17.60	19.90	0.00	0.00	0.00	0.00
SJMM	1	20.90	0.00	0.00	0.00	22.55	22.60	0.00	0.00	0.00	0.00
MNGM	2	22.58	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
SMAM	1	20.35	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
PDCM	1	20.15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
SMGM	1	18.80	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
ESPM	6	20.56	2.78	1.13	13.53	17.78	23.34	18.10	23.25	17.64	23.48
SFXM	1	18.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Table 4.18 - Males of Eastern Brazil. Levels of Probability of Significant Differences Between Samples. Across Canines.

Sample	p	SNK	
Coastal Transect			
Smgm/ILHM	.4		
ILHM/ESPM		*	break
GBTM/Smam	.2		
GBTM/Hngm	.8		
GBTM/Litm	.9		
GBTM/Banm	.3		
BFLM/Smam	.3		
BFLM/Hngm	.2		
SCAM/Banm	.2		
SCAM/Litm	.8		
SCAM/Hngm	.9		
Ilheus-Bananal Transect			
ILHM/ESPM		*	break
ESPM/ZMHM		*	break
ZMHM/Sjmm	.4		
ZMHM/Vapm	.7		
Vapm/COTM	.4		
COTM/Banm	.9		
Litoral-Lins Transect			
Litm/COTM	.4		
COTM/Capm	.05	*	break
COTM/Pdcm	.9		
COTM/Itum	.8		
COTM/Linm	.2		
Floresta da Tijuca-Lins Transect			
GBTM/BFLM		NS	
BFLM/TERM		NS	
TERM/Sjmm	.3		
TERM/ZMHM		*	break
ZMHM/Pdcm	.1		
ZMHM/Itum	.4		
ZMHM/Linm	.05	*	break

(continued)

Table 4.18 (continuation)

Santa Catarina-Lins Transect

SCAM/Banm	.2
SCAM/Linm	.9

specimen, is very large, and the break with Cotia does not impede the continuation of the analysis along the transect, which is more sweeper-like than a straight line.

d. Guanabara-Lins Transect - Guanabara, Baixada Fluminense, Terezopolis and Sao Joao Marcos form a set of related samples. Sao Joao Marcos has a lower probability when compared with Zona da Mata than with Terezopolis. This latter has a break with Zona da Mata. Along the transect, the Zona da Mata has links with Pocos de Caldas and Ituverava. However, Lins has a clear break with it.

e. Santa Catarina-Lins Transect - The transect is fairly homogeneous, Lins and Bananal belonging to the same set of Santa Catarina.

e. Summary - The following sets can be identified: Ilheus and Sao Miguel; Espirito Santo; the whole litoral localities plus the Baixada and Terezopolis extending further west to all hinterland in Sao Paulo; and finally the Zona da Mata, varying clinaly toward the south and linked with the hinterland of Minas. Intermediate populations exist as Macae and Vale do Paraiba. Table 4.18 brings together all probabilities along the transects.

4. Breadth across Molars (Table 4.19)

a. Coastal Transect - Table 4.19 brings together all statistics of the samples for this character. Table 4.20 shows the levels of probabilities of comparison between the samples along the transects.

In this first transect, the Ilheus and Sao Miguel appear together again. This set has a break with the Southern samples. Macae is nearer to Espirito Santo than to Baixada and Guanabara.

TABLE 4.19 ACROSS MOLARS EASTERN BRAZIL MALES BASIC STATISTICS

SAMP	N	MEAN	SDEV	SERR	CV	RANGE		AVSDEV		CONFL	
SCAM	5	29.22	2.73	1.22	9.34	25.10	33.35	0.00	0.00	0.00	0.00
COTM	16	29.79	1.85	0.46	6.22	28.50	32.35	27.94	31.64	28.80	30.77
GBTM	7	28.86	1.56	0.59	5.40	26.05	30.75	27.30	30.42	27.47	30.26
TERM	6	30.23	0.73	0.30	2.43	29.10	30.90	29.50	30.96	29.50	30.97
ZMMM	10	29.58	1.21	0.38	4.09	27.65	31.10	28.37	30.79	28.73	30.43
ILHM	17	30.80	2.05	0.29	7.02	28.80	32.50	28.75	32.85	30.18	31.42
BFLM	6	31.06	1.00	0.41	3.22	29.65	32.30	30.06	32.06	30.06	32.06
BANM	4	31.38	0.00	0.00	0.00	30.00	32.25	0.00	0.00	0.00	0.00
LITM	3	29.77	0.00	0.00	0.00	27.85	32.10	0.00	0.00	0.00	0.00
CAPM	1	28.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
LINM	1	31.35	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
VAPM	4	30.04	0.00	0.00	0.00	29.60	30.25	0.00	0.00	0.00	0.00
SFXM	1	29.20	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
ITUM	3	30.80	0.00	0.00	0.00	29.95	31.70	0.00	0.00	0.00	0.00
SJMM	1	29.20	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
MNGM	2	29.50	0.00	0.00	0.00	29.15	29.85	0.00	0.00	0.00	0.00
SMAN	1	30.30	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
PDCM	1	30.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
ESPM	6	30.09	0.89	0.36	29.60	29.20	30.98	29.05	31.40	29.16	31.03
SMGM	1	31.15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Table 4.20 - Males of Eastern Brazil. Levels of Probability of Significant Differences Between Samples. Across Molars

Sample	p	SNK	
Coastal Transect			
Smgm/ILHM	.5		
ILHM/ESPM		*	break
ESPM/Smam	.8		
Smam/GBTM	.7		
GBTM/Mngm	.9		
GBTM/LItm	.9		
GBTM/Banm	.3		
Smam/BFLM	.9		
BFLM/Mngm	.05	*	break
Mngm/SCAM	.8		
Litm/SCAM	.7		
Banm/SCAM	.9		
Ilheus-Bananal Transect			
ESPM/ZMMM		*	break
ZMMM/Sjmm	.02	*	break
ZMMM/Vapm	.01	*	break
Vapm/COTM	.3		
COTM/Banm	.9		
Litoral-Lins Transect			
Litm/COTM	.7		
COTM/Capm	.9		
COTM/Pdecm	.7		
COTM/Itum	.9		
COTM/Linm	.7		
Floresta da Tijuca-Lins Transect			
GBTM/BFLM		NS	
BFLM/TERM		NS	
TERM/Sjmm	.02	*	break
TERM/ZMMM		*	break
ZMMM/Sjmm	.02	*	break
ZMMM/Pdcm	.05	*	break

(continued)

Table 4.20 (continuation)

Santa Catarina-Lins Transect	
SCAM/Banm	.9
SCAM/Linm	.9

Down South from Guanabara up to Santa Catarina, the pattern is all similar to the previous character (CAN). However, the Baixada has a break with the samples at the South, Mangaratiba.

b. Ilheus Bananal Transect - Espirito Santo is isolated north and south. The same applies to Zona da Mata. From the Vale do Paraiba southwards, there are no significant differences.

c. Litoral- Lins Transect - This is a fairly homogeneous transect with no apparent differentiation.

d. Guanabara-Lins Transect - There is a set of Baixada, Guanabara, Terezopolis and Sao Joao Marcos, which is different from Zona da Mata. In this character, Zona da Mata is isolated in all transects.

e. Santa Catarina-Lins - Another homogeneous transect.

f. Summary - The grouping in this character is somewhat clear-cut: the first set is Ilheus and Sao Miguel; the second, Espirito Santo with Macae as intergrading locality between this set and the third, formed by all localities further south, excepting Zona da Mata, which forms the fourth and last set.

5. Breadth of Palatal Shelf (Tables 4.21 and 4.22)

a. Coastal Transect - Ilheus and Sao Miguel form a set, Espirito Santo and Macae another, Guanabara is isolated from all other samples. The baixada has a low probabilitiy with Mangaratiba and the Litoral. But further south the transect is homogeneous, probabilities varying without any link to the distance.

TABLE 4.21 PALATAL SHELF EASTERN BRAZIL MALES BASIC STATISTICS

SAMP	N	MEAN	SDEV	SERR	CV	RANGE		AVSDEV		CONFL	
SCAM	6	17.99	1.31	0.53	7.26	16.70	20.10	17.99	20.61	16.69	19.30
COTM	16	17.45	0.89	0.22	5.08	15.35	19.45	16.56	18.34	16.98	17.92
GBTM	5	17.83	0.86	0.38	4.80	16.65	18.55	16.97	18.69	16.85	18.81
TERM	6	17.54	1.03	0.42	5.91	16.20	19.05	16.51	18.57	16.51	18.58
ZMMM	9	17.66	0.69	0.23	3.91	16.80	19.15	16.97	18.35	17.14	18.18
ILHM	18	17.96	1.26	0.30	7.03	15.20	19.98	16.70	19.22	17.34	18.59
BFLM	6	17.59	1.19	0.49	6.78	16.10	18.90	17.58	18.77	16.38	18.77
BANM	4	18.68	0.00	0.00	0.00	18.20	19.25	0.00	0.00	0.00	0.00
LITM	2	17.10	0.00	0.00	0.00	16.90	17.30	0.00	0.00	0.00	0.00
CAPM	1	16.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
LINM	2	17.98	0.00	0.00	0.00	17.60	18.35	0.00	0.00	0.00	0.00
SFXM	1	17.35	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
ITUM	3	18.27	0.00	0.00	0.00	17.60	18.70	0.00	0.00	0.00	0.00
VAPM	2	17.05	0.00	0.00	0.00	16.80	17.30	0.00	0.00	0.00	0.00
SJMM	1	17.50	0.00	0.00	0.00	17.05	18.90	0.00	0.00	0.00	0.00
MNGM	2	17.98	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
SMAM	1	17.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
PDCM	1	18.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
ESPM	5	17.07	0.32	0.14	1.87	16.70	17.40	16.75	17.39	16.68	17.46
SMGM	1	17.10	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Table 4.22 - Males of Eastern Brazil. Levels of Prbability of Significant Differences Between Samples. Palatal Shelf.

Sample	p	SNK	
Coastal Transect			
Smgm/ILHM	.9		
ILHM/ESPM	.05	*	break
ESPM/Smam	.3		
Smam/GBTM	.01	**	break
GBTM/Mngm	.001	***	break
Smam/BFLM	.05	*	break
BFLM/Mngm	.1		
BFLM/Litm	.2		
BFLM/Banm	.8		
SCAM/Banm	.5		
SCAM/Litm	.8		
SCAM/Mngm	.1		
Ilheus-Bananal Transect			
ESPM/ZMMM	.4		
ZMMM/Sjmm	.3		
ZMMM/Vapm	.6		
Vapm/COTM	.8		
COTM/Banm	.2		
Litoral-Lins Transect			
Litm/COTM	.7		
COTM/Capm	.1		
COTM/Pdcm	.7		
COTM/Itu	.6		
COTM/Linm	.9		
Floresta da Tijuca-Lins Transect			
GBTM/BFLM		*	break
BFLM/TERM		*	break
TERM/Sjmm	.7		
TERM/ZMMM		*	break
ZMMM/Pdcm	.7		
ZMMM/Itum	.6		
ZMMM/Linm	.6		

(continued)

Table 4.22 - (continuation)

Santa Catarina-Lins Transect	
SCAI/Banm	.5
SCAM/Linm	.1

b. Ilheus-Bananal Transect - Zona da Mata is linked to Espirito Santo. There is no difference between Zona da Mata and Sao Joao Marco and Vale do Paraiba. The differentiation seems to be clinal, Cotia being different from Zona da Mata, but without differentiation with Vale do Paraiba and Bananal.

c. Litoral-Lins Transect - A homogeneous transect, with the usual low value between Campinas and Cotia, due to the large size of the Campinas specimen.

d. Guanabara-Lins Transect - Guanabara, Baixada and Terezopolis show differences among them. Sao Joao Marcos has no difference to both Terezopolis and Zona da Mata. The samples further west belong to the same set of Zona da Mata.

e. Summary - This character has low variability intra-locality, but is well differentiated along the transects. The grouping can be seen as follows: Ilheus and Sao Miguel; Espirito Santo, Zona da Mata, Macae, Pocos de Caldas, Ituverava and Lins; Guanabara; Terez-opolis and Sao Joao Marcos; Baixada Fluminense, Litoral, Mangaratiba, Bananal, Cotia and Santa Catarina.

6. Length of Maxilary Tooth row (Table 4.23)

The Student -Newman Keuls test for this character was found not significant for the differences among the means of all samples, but Santa Catarina. No further analysis was made.

7. Length of Upper Molar Series (Table 4.24)

As in the character above, the test of differences among

TABLE 4.23 MAXILLARY EASTERN BRAZIL MALES BASIC STATISTICS

SAMP	N	MEAN	SDEV	SERR	CV	RANGE		AVSDEV		CONFL	
SCAM	5	41.73	1.24	0.55	2.96	40.65	43.85	40.49	42.97	40.31	43.15
COTM	16	41.58	1.12	0.28	2.70	38.90	43.70	40.46	42.70	40.99	42.18
GBTM	7	41.06	1.55	0.59	3.78	38.15	42.70	39.51	42.61	39.67	42.44
TERM	7	41.71	1.72	0.65	4.13	39.20	44.40	39.99	43.43	40.17	43.26
ZMMM	10	42.24	1.61	0.51	5.71	39.35	44.30	40.63	43.85	41.11	43.38
ILHM	15	42.72	1.95	0.50	4.57	39.55	46.35	40.77	44.67	41.65	43.79
BFLM	7	42.02	1.27	0.48	3.03	39.75	43.40	40.75	43.29	40.89	43.16
BANM	4	43.14	0.00	0.00	0.00	40.50	44.95	0.00	0.00	0.00	0.00
LITM	2	40.83	0.00	0.00	0.00	39.30	42.35	0.00	0.00	0.00	0.00
CAPM	1	42.30	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
LINM	1	43.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
SFXM	1	41.30	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
ITUM	3	41.63	0.00	0.00	0.00	41.05	42.70	0.00	0.00	0.00	0.00
VAPM	4	40.75	0.00	0.00	0.00	39.10	43.20	0.00	0.00	0.00	0.00
SJMM	1	41.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
MNGM	2	40.60	0.00	0.00	0.00	39.40	41.80	0.00	0.00	0.00	0.00
SMAM	1	41.45	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
PDCM	1	40.20	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
ESPM	5	42.19	1.31	0.59	3.11	40.85	43.85	40.88	43.50	40.55	43.83
SMGM	1	41.45	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

TABLE 4.24 MOLAR SERIES EASTERN BRAZIL MALES BASIC STATISTICS

SAMP	N	MEAN	SDEV	SERR	CV	RANGE		AVSDEV		CONFL	
SCAM	5	19.56	0.50	0.22	2.54	0.00	0.00	19.06	20.06	25.80	31.97
COTM	15	18.76	1.30	0.34	6.93	18.95	20.10	17.46	20.06	18.04	19.48
GBTM	7	18.91	0.51	0.19	2.72	14.55	19.85	18.40	19.42	18.45	19.37
TERM	8	18.97	0.80	0.28	4.22	17.35	20.05	18.17	19.77	18.32	19.62
ZMMM	10	19.30	0.70	0.22	3.64	18.40	20.60	18.60	20.00	18.81	19.80
ILHM	17	19.74	0.80	0.19	4.04	18.15	20.80	18.94	20.54	19.33	20.14
BFLM	7	19.28	0.70	0.26	3.62	18.50	20.00	18.58	19.98	18.66	19.90
BANM	4	19.90	0.00	0.00	0.00	19.60	20.20	0.00	0.00	0.00	0.00
LITM	3	19.68	0.00	0.00	0.00	19.15	20.35	0.00	0.00	0.00	0.00
CAPM	1	18.75	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
LINM	1	19.15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
SFXM	1	19.15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
ITUM	3	19.63	0.00	0.00	0.00	19.40	19.90	0.00	0.00	0.00	0.00
VAPM	3	20.08	0.00	0.00	0.00	17.80	22.75	0.00	0.00	0.00	0.00
SJMM	1	17.85	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
MNGM	1	18.30	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
SNAM	1	19.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
PDCM	1	18.55	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
ESPM	5	18.95	0.58	0.26	3.08	18.35	19.65	18.37	19.53	17.33	20.57
SMGM	1	18.55	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

the means gave a non-significant reslut, except for the Espirito Santo sample. Therefore, no other analysis was made.

8. Breadth of Rostrum across Jugals (Table 4.25 and 4.26)

a. Coastal Transect - From Sao Miguel to Macae, there is no break. Guanabara has a break with Macae and with Espirito Santo. The Baixada Fluminense has no difference to Macae but is significantly different from Guanabara. The three samples further south have low values of probability of significant difference to both Guanabara and Baixada Fluminense.

Santa Catarina is isolated from all other samples.

b. Ilheus-Bananal Transect - This transect is homogeneous, Sao Joao Marcos with a higher probability of significance, but still not breaking the transect.

c. Litoral-Lins Transect - Cotia and Campinas have the highest probability, Pocos de Caldas being the nearest sample to Cotia. The rest of the comparisons are at similar levels.

d. Guanabara-Lins Transect - Guanabara, Baixada are different. Sao Joao Marcos is significantly different from Terezopolis. However Zona da Mata is not different from Sao Joao Marcos and from Terezopolis. The rest of the transect varies in the probability values, but there are no breaks.

e. Santa-Catarina Transect - Santa Catarina has a break when compared to Bananal.

f. Summary - This character has some odd differentiations. All samples west of the Serra do Mar can be considered together with

TABLE 4.25 ROSTRUM ACROSS JUGALS EASTERN BRAZIL MALES BASIC STATISTICS

SAMP	N	MEAN	SDEV	SERR	CV	RANGE		AVSDEV		CONFL	
SCAM	6	28.88	3.09	0.60	9.19	25.80	32.70	25.79	31.97	25.80	31.97
COTM	17	25.66	2.52	0.61	9.81	22.90	32.60	23.14	28.18	24.37	29.94
GBTM	7	28.24	2.44	0.92	8.64	27.95	31.05	25.80	30.68	26.05	30.42
TERM	10	27.52	1.29	0.41	4.69	25.05	29.75	26.23	28.81	26.62	28.43
ZMMM	10	26.61	3.52	1.11	13.22	18.85	31.00	23.09	30.13	24.14	29.09
ILHM	18	28.46	2.81	0.66	9.90	23.90	32.50	25.65	31.27	27.06	29.85
BFLM	7	26.34	3.79	1.43	14.41	19.00	30.50	22.55	30.13	22.94	29.73
BANM	4	28.58	0.00	0.00	0.00	26.70	29.85	0.00	0.00	0.00	0.00
LITM	3	26.03	0.00	0.00	0.00	24.55	27.30	0.00	0.00	0.00	0.00
CAPM	1	32.60	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
VAPM	4	26.08	0.00	0.00	0.00	24.00	28.20	0.00	0.00	0.00	0.00
LINM	1	26.15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
SFXM	1	26.15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
ITUM	3	25.60	0.00	0.00	0.00	24.60	26.40	0.00	0.00	0.00	0.00
SJMM	1	31.65	0.00	0.00	0.00	29.80	30.90	0.00	0.00	0.00	0.00
MNGM	2	30.35	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
SMAM	1	28.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
PDCM	1	26.65	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
ESPM	6	28.05	3.47	1.42	12.37	25.15	32.90	24.58	31.52	24.40	31.70
SMGM	1	21.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Table 4.26 - Males of Eastern Brazil. Levels of Probability of Significant Difference Between Samples. Rostrum across Jugals.

Sample	p	SNK	
Coastal Transect			
Smgm/ILHM	.9		
ILHM/ESPM	.4		
ESPM/Smam	.05	*	break
Smam/GBTM	.9		
GBTM/Litm	.9		
GBTM/Banm	.6		
Smam/BFLM	.9		
BFLM/Mngm	.9		
BFLM/Litm	.8		
BFLM/Banm	.9		
SCAM/Banm	.05	*	break
Ilheus-Baranal Transect			
ESPM/ZMMM		NS	
ZMMM/Sjmm	.1		
ZMMM/Vapm	.8		
Vapm/COTM	.7		
COTM/Banm	.7		
Litoral-Lins Transect			
Litm/COTM	.6		
COTM/Capm	.1		
COTM/Pdcm	.8		
COTM/Itum	.5		
COTM/Linm	.5		
Floresta da Tijuca-Lins Transect			
GBTM/BFLM		*	break
BFLM/TERM		*	break
TERM/Sjmm	.001	***	break
TERM/ZMMM		NS	
ZMMM/Sjmm	.1		
ZMMM/Pdcm	.3		
ZMMM/ITUM	.7		
ZMMM/Linm	.5		

(continued)

Table 4.26 - (continuation)

Santa Catarina-Lins Transect			
SCAM/Banm	.05	*	break

Espirito Santo and the Northeast samples. Even the Baixada Fluminense has a link with this set through Macae. On the other hand, Guanabara is isolated but can be considered together with the Litoral samples, and through them with the Baixada. This mosaic is difficult to analyse, neighbouring localities are dissimilar, but share low probabilities of significant differences with those further away.

9. Greatest Breadth of Nasals

a. Coastal Transect - There is the usual break between Ilheus and Espirito Santo. Macae is intergradating between the different Guanabara and Baixada and Espirito Santo. Further South there is no differentiation.

However, Santa Catarina has significant differences with both Guanabara and Baixada Fluminense.

b. Ilheus-Bananal Transect - Zona da Mata does not belong to northern samples and is different from Sao Joao Marcos. As usual Vale do Paraiba belongs to both Zona da Mata and Cotia.

c. Litoral-Lins Transect - Lins and Campinas show significant differences with Cotia. Campinas is the usual single large individual.

d. Guanabara-Lins Transect - Guanabara and Baixada Fluminense belong to the same set. Terezopolis is isolated from all samples. Zona da Mata shows the usual pattern further west with the exception of Lins.

e. Santa Catarina-Lins Transect - Lins is isolated as well in this transect.

TABLE 4.27 BREADTH OF NASALS EASTERN BRAZIL MALES BASIC STATISTICS

SAMP	N	MEAN	SDEV	SERR	CV	RANGE		AVSDEV		CONFL	
SCAM	6	15.98	1.47	0.60	9.19	14.15	18.25	14.51	17.45	14.52	17.45
COTM	17	14.82	1.78	0.43	12.05	13.10	20.05	13.04	16.60	13.90	15.73
GBTM	7	15.85	2.65	1.00	16.72	12.70	20.60	13.20	18.50	13.48	18.22
TERM	12	16.32	1.36	0.39	8.31	13.30	17.65	14.96	17.68	15.47	17.17
ZMMM	9	16.37	1.29	0.43	7.88	14.05	18.20	15.08	17.66	15.39	17.34
ILHM	18	16.10	1.92	0.45	11.90	13.50	18.50	14.18	18.02	15.15	17.05
BFLM	7	15.74	1.28	0.48	8.15	13.20	16.80	14.46	17.02	14.59	16.88
BANM	4	16.13	0.00	0.00	0.00	14.80	17.40	0.00	0.00	0.00	0.00
LITM	3	15.35	0.00	0.00	0.00	13.50	17.75	0.00	0.00	0.00	0.00
CAPM	1	20.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
LINM	1	20.20	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
SFXM	1	14.70	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
VAPM	4	14.76	0.00	0.00	0.00	13.25	16.90	0.00	0.00	0.00	0.00
SJMM	1	20.60	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
MNGM	2	17.33	0.00	0.00	0.00	16.00	18.65	0.00	0.00	0.00	0.00
SMAM	1	16.55	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
PDCM	1	14.80	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
ESPM	6	15.80	2.25	0.92	14.21	13.05	18.90	13.58	18.08	13.46	18.20
SMGM	1	14.65	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
ITUM	3	17.38	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Table 4.28 - Males of Eastern Brazil. Levels of Probability of Significant Differences between Samples. Breadth of Nasals

Sample	p	SNK	
Coastal Transect			
Smgm/ILHM	.9		
ILHM/ESPM		*	break
ESPM/Smam	.4		
ESPM/GBTM		*	break
Smam/GBTM	.5		
GBTM/Mngm	.9		
GBTM/Linm	.5		
GBTM/Banm	.8		
GBTM/SCAM		*	break
Smam/BFLM	.9		
BFLM/Mngm	.5		
BFLM/Litm	.6		
BFLM/Banm	.6		
BFLM/SCAM		*	break
Ilheus-Bananal Transect			
ESPM/ZMMM		*	break
ZMMM/Sjmm	.01	**	break
ZMMM/Vapm	.5		
Vapm/COTM	.4		
COTM/Banm	.9		
Litoral-Lins Transect			
Litm/COTM	.6		
COTM/Capm	.01	*	break
COTM/Pdecm	.4		
COTM/Itum	.4		
COTM/Linm	.01	**	break

(continued)

Table 4.28 - (continuation)

Floresta da Tijuca-Lins Transect			
GBTM/BFLM		NS	
BFLM/TERM		*	break
TERM/Sjmm	.01	**	break
TERM/ZMMM		*	break
ZMMM/Pdcm	.6		
ZMMM/Itum	.9		
ZMMM/Linm	.01	**	break
Santa Catarina-Lins Transect			
SCAM/Banm	.3		
SCAM/Linm	.02	*	break

f. Summary - The following grouping may be suggested- Sao Miguel and Ilheus; Espirito Santo and Macae; Baixada and Guanabara with the litoral localities further south, Santa Catarina being the other extreme which is differentiated; Cotia asa somewhat intermediate sample in a mosaic and being the extreme which is differentiated in the Zona da Mata set; and finally, Lins, isolated from all other samples.

10. Mandibular Length (Table 4.29 and 4.30)

a. Coastal Transect - Ilheus and Sao Miguel form a set isolated from Espirito Santo. The latter has a break with Macae. Southward there is no differntiation at a significant level. Santa Catarina Guanabara and the Baixada are in the same non-significant range. Therefore, I analysed only Guanabara in relation to localities further south.

b. Ilheus - Bananal Transect - Zona da Mata is significantly different from Espirito Santo. It is different from Sao Joao Marcos as well. As usual, it has no difference with the Vale do Paraiba, which in turn has no difference with Cotia. But Cotia and Zona da Mata are different. Cotia has a low level of significance with Banaral.

c. Guanabara-Lins Transect - Guanabara, Baixada and Terezopolis form a set. The latter is different from Sao Joao Marcos, and they are all different from Zona da Mata. The Zona da Mata has the usual non-significant differences with the localities further west.

d. Santa Catarina-Lins - An homogeneous transect.

TABLE 4.29 MANDIBLE EASTERN BRAZIL MALES BASIC STATISTICS

SAMP	N	MEAN	SDEV	SERR	CV	RANGE		AVSDEV		CONFL	
SCAM	7	84.79	10.33	3.91	12.19	68.10	99.85	74.45	95.12	75.22	94.35
COTM	16	81.01	5.20	1.30	6.42	72.85	95.95	75.81	86.21	78.25	83.77
GBTM	6	86.09	4.82	1.97	5.60	77.70	90.80	81.27	90.91	81.28	90.90
TERM	8	84.34	5.14	1.82	6.09	75.10	90.20	79.20	89.48	80.15	88.53
ZMMM	9	87.74	5.80	1.93	6.61	71.55	90.20	81.94	93.54	83.37	92.12
ILHM	18	89.21	6.45	1.52	7.24	79.95	98.30	82.76	95.66	86.01	92.40
BFLM	6	87.75	2.68	1.10	3.06	84.30	90.80	85.07	90.43	85.07	90.43
BANM	3	86.95	0.00	0.00	0.00	82.20	90.75	0.00	0.00	0.00	0.00
LITM	3	79.98	0.00	0.00	0.00	73.95	85.70	0.00	0.00	0.00	0.00
CAPM	1	95.95	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
LINM	1	92.55	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
SFXM	1	79.45	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
ITUM	3	83.03	0.00	0.00	0.00	80.70	86.05	0.00	0.00	0.00	0.00
VAPM	5	81.53	3.97	1.78	4.87	76.65	87.30	77.56	85.50	70.51	92.55
SJMM	1	100.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
MNGM	2	90.28	0.00	0.00	0.00	87.75	92.80	0.00	0.00	0.00	0.00
SMAM	1	86.70	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
PDCM	1	85.55	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
ESPM	6	86.50	6.32	2.58	7.31	79.45	93.60	80.18	92.82	79.86	93.14
SMGM	1	84.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Table 4.30 - Males of Eastern Brazil. Levels of Probability of Significant Differences Between Samples. Mandibular Lenght

Coastal Transect			
Smgm/ILHM	.9		
ILHM/ESPM		*	break
ESPM/Smam	.001	***	break
Smam/GBTM	.4		
GBTM/BFLM		NS	
GBTM/Mngm	.9		
GBTM/Litm	.5		
GBTM/Banm	.4		
GBTM/SCAM		NS	
Ilheus-Bananal Transect			
ILHM/ESPM		*	break
ESPM/ZMMM		*	break
ZMMM/Sjmm	.05	*	break
ZMMM/Vapm	.7		
COTM/Banm	.6		
Litoral-Lins Transect			
Litm/COTM	.6		
COTM/Capm	.01	**	break
COTM/Pdcm	.8		
COTM/Itum	.8		
COTM/Linm	.1		
Floresta da Tijuca-Lins Transect			
GBTM/BFLM		NS	
BFLM/TERM		NS	
TERM/Sjmm	.01	**	break
TERM/ZMMM		*	break
ZMMM/Pdcm	.6		
ZMMM/Itum	.9		
ZMMM/Linm	.9		
Santa Catarina-Lins Transect			
SCAM/Banm	.8		
SCAM/Linm	.9		

e. Summary - The grouping can be suggested to be: Ilheus and Sao Miguel; Espirito Santo; Santa Catarina, litoral south, Guanabara Baixada and Terezopolis, Cotia and localities further west and Vale do Paraiba sharing similarities with the last group, Zona da Mata.

4.8.2 Eastern Brazil: Females

1. Condylo-Basal Length (Tables 4.31 and 4.32)

a. Coastal Transect - Ilheus goes without difference up to Baixada, but the latter is different from Casimiro de Abreu, which has no significant difference with Guanabara. Guanabara is different from Baixada and from the Litoral de Sao Paulo but not from Mangaratiba which is different from Baixada. Santa Catarina is different from the Litoral de Sao Paulo.

b. Ilheus-Cotia Transect - The transect is homogeneous, but Cotia has a significant difference with Zona da Mata, as well as with Ilheus.

c. Litoral-Campinas Transect - No differentiation along the transect.

d. Guanabara-Zona da Mata Transect - Terezopolis and Baixada belong to the same set of Zona da Mata. Guanabara is different from the others.

e. Summary - From Ilheus to Cotia there is some homogeneity, the Vale do Paraiba being the intergrading zone between this set and the second, composed by Guanabara and the litoral. Santa Catarina and Bananal seems to form another set.

TABLE 4.31 CONDYLO BASAL EASTERN BRAZIL FEMALES BASIC STATISTICS

SAMP	N	MEAN	SDEV	SERR	CV	RANGE		AVSDEV		CONFL	
COTF	9	91.90	3.90	1.30	4.24	84.30	97.50	88.00	95.80	88.96	94.84
LITF	7	94.58	4.89	1.85	5.17	0.00	0.00	89.69	99.47	90.21	98.95
TERF	10	93.08	6.00	1.90	6.45	85.75	2.90	87.08	99.08	88.54	97.32
ZMMF	6	89.50	3.21	1.31	3.59	84.20	93.70	86.37	92.79	86.37	92.79
ILHF	5	100.40	5.69	2.80	5.67	92.15	6.25	94.71	6.09	93.86	6.94
BFLF	5	89.82	2.29	1.02	2.55	87.15	92.20	0.00	0.00	87.19	92.45
SCAF	1	102.10	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
BANF	2	92.13	0.00	0.00	0.00	87.70	96.55	0.00	0.00	0.00	0.00
CAPF	2	101.58	0.00	0.00	0.00	97.30	7.85	0.00	0.00	0.00	0.00
VAPF	3	89.65	0.00	0.00	0.00	86.00	93.15	0.00	0.00	0.00	0.00
MNGF	1	99.90	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
CASF	1	101.85	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
ESPF	2	94.23	0.00	0.00	0.00	91.10	97.35	0.00	0.00	0.00	0.00
GBTF	50	94.91	3.30	1.48	3.48	91.00	3.00	91.61	98.21	91.12	98.70

Table 4.32 - Females of Eastern Brazil. Levels of Probability of Significant Differences Between Samples. Condylo-basal.

Sample	p	SNK	
Coastal Transect			
ILHF/Espf	.3		
ILHF/Casf	.05	*	break
GBTF/Casf	.05	*	break
GBTF/Mngf	.3		
BFLF/Mngf	.001	***	break
BFLF/Casf	.001	***	break
LITF/Mngf	.3		
LITF/Banf	.5		
LITF/Scaf	.05	*	break
Ilheus-Bananal Transect			
Espf/ZMMF	.4		
ZMMF/Vapf	.5		
Vapf/COTF	.5		
COTF/Banf	.02	*	break
Litoral-Campinas Transect			
LITF/COTF		*	break
COTF/Capf	.001	***	break
Floresta da Tijuca-Zona da Mata			
GBTF/BFLF		*	break
BFLF/TERF		NS	
TERF/ZMMF		NS	

2. Palatal Length - (Tables 4.33 and 4.34)

a. Coastal Transect - There is only one break from the t test, between Mangaratiba and Baixada. The results of the SNK test together with the t test, suggests that the localities between the major samples are intergrading zones. The results of the analysis are not very clear.

b. Ilheus-Bananal Transect -The transect goes without differences but again, Cotia is different from the major samples further north.

c. Litoral-Campinas Transect - No differentiation

d. Guanabara-Zona da Mata - Baixada Fluminense and Terezopolis are significantly different from both Zona da Mata and Terezopolis.

e. Summary - The grouping of localities can be construed in the following way: Ilheus to Guanabara, intergrading, with the extremes with differences; Ilheus to Bananal, Ilheus being different from Cotia; Santa Catarina, Bananal, Litoral and Guanabara with Cotia and Bananal as somewhat linked and intergrading through the Vale do Paraiba with Ilheus.

3. Zygomatic Breadth (Tables 4.35 and 4.36)

a. Coastal Transect - Ilheus, Baixada and Guanabara have no differences. Casimiro de Abreu is, however, different from every one else. Mangaratiba is isolated as well. From Litoral further South, there is no differentiation.

b. Ilheus-Bananal Transect - The usual pattern in this transect appears, with the Vale do Paraiba being the intergradation area.

TABLE 4.33 PALATAL LENGHT EASTERN BRAZIL FEMALES BASIC STATISTICS

SAMP	N	MEAN	SDEV	SERR	CV	RANGE		AVSDEV		CONFL	
COTF	9	57.78	2.56	0.85	4.44	54.40	60.85	55.22	60.34	55.85	59.72
LITF	7	59.80	2.41	0.91	4.04	54.60	61.40	57.39	62.21	57.64	61.96
TERF	9	57.84	3.55	1.18	3.55	53.20	62.80	54.29	61.39	55.16	60.51
ZMMF	6	56.75	1.89	0.77	3.34	53.65	59.40	54.86	58.64	54.86	58.64
ILHF	5	61.78	3.00	1.34	4.86	58.80	66.70	58.78	64.78	58.33	65.23
BFLF	5	56.76	1.40	0.63	2.47	55.05	58.90	55.36	58.16	55.15	58.37
SCAF	2	62.90	0.00	0.00	0.00	62.80	63.00	0.00	0.00	0.00	0.00
BANF	2	59.28	0.00	0.00	0.00	56.30	62.25	0.00	0.00	0.00	0.00
CAPF	2	56.28	0.00	0.00	0.00	50.70	61.85	0.00	0.00	0.00	0.00
VAPF	3	55.95	0.00	0.00	0.00	54.50	58.25	0.00	0.00	0.00	0.00
MNGF	1	62.95	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
CASF	1	60.80	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
ESPF	2	57.05	0.00	0.00	0.00	57.05	61.60	0.00	0.00	0.00	0.00
GBTF	5	59.21	2.10	0.94	0.00	55.85	61.20	57.11	61.31	56.80	61.62

Table 4.34 - Females of Eastern Brazil. Levels of Probability of Significant Differences Between Samples. Palatal Lenght.

Sample	p	SNK	
Coastal Transect			
ILHF/Espf	.3		
ILHF/Casf	.7		
Casf/GBTF	. 9		
GBTF/Espf	.7		
GBTF/Mnfg	.2		
BFLF/Casf	.1		
BFLF/Espf	.6		
BFLF/Mngf	.01		break
LITF/Mngf	.5		
LITF/Banf	.6		
LITF/Scaf	.5		
Ilheus-Bananal Transect			
Espf/ZMMF	.6		
ZMMF/Vapf	.8		
Vapf/COTF	.9		
COTF/Banf	.7		
LItoral-Campinas Transect			
LITF/COTF		NS	
COTF/Capf	.7		
Floresta da Tijuca-Zona da Mata Transect			
GBTF/BFLF		*	break
BFLF/TERF		NS	
TERF/ZMMF		*	break

TABLE 4.35 ZYGOMATIC EASTERN BRAZIL FEMALES BASIC STATISTICS

SAMP	N	MEAN	SDEV	SERR	CV	RANGE		AVSDEV		CONFL	
COTF	10	46.92	2.03	0.64	4.32	44.10	51.10	44.89	48.95	45.49	48.34
LITF	7	49.36	2.85	1.08	5.78	44.10	52.95	46.51	52.21	46.81	51.91
TERF	9	49.75	5.63	1.88	11.32	43.40	55.30	44.12	55.38	45.50	54.00
ZMMF	7	46.56	1.77	0.67	3.81	44.90	49.20	44.79	48.33	44.97	48.14
ILHF	5	50.65	2.92	1.31	5.77	46.40	53.80	47.73	53.57	47.29	54.01
BFLF	5	45.90	1.96	0.88	4.28	43.15	47.55	43.94	47.86	43.64	48.16
GBTF	5	51.55	3.10	0.79	3.41	48.80	53.10	48.45	54.65	49.53	53.57
SCAF	1	50.70	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
BANF	2	46.45	0.00	0.00	0.00	45.10	47.80	0.00	0.00	0.00	0.00
CAPF	2	48.10	0.00	0.00	0.00	46.25	49.95	0.00	0.00	0.00	0.00
VAPF	3	46.55	0.00	0.00	0.00	43.40	50.55	0.00	0.00	0.00	0.00
MNGF	1	57.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
CASF	1	58.70	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
ESPF	2	49.68	0.00	0.00	0.00	45.10	54.25	0.00	0.00	0.00	0.00

Table 4.36 - Females of Eastern Brazil. Levels of Probabity of Significant Differences Betwee Samples. Zygomatic Breadth.

Sample	p	SNK	
Coastal Transect			
ILHF/Espf	.5		
ILHF/Casf	.05		break
Casf/GBTF	.01		break
GBTF/Mngf	.02		break
BFLF/Casf	.001		break
BFLF/Mngf	.001		break
LITF/Mngf	.05		break
LITF/BAnf	.7		
LITF/Scaf	.8		
Ilheus-Bananal Transect			
Espf/ZMMF	.5		
ZMMF/Vapf	.4		
COTF/Vapf	.5		
COTF/Banf	.5		
Litoral-Campinas Transect			
LITF/COTF		*	break
COTF/Capf	.5		
Floresta da Tijuca-Zona da Mata Transect			
GBTF/BFLF		NS	
BFLF/TERF		*	break
TERF/ZMMF		*	break

Bananal belongs to the same set as Cotia.

c. Litoral-Campinas - Litoral is different from Cotia. Campinas and Cotia form a single set.

d. Guanabara-Zona da Mata Transect - Terezopolis is isolated from both Guanabara/Baixada and Zona da Mata.

e. Summary - All localities from Ilheus to Guanabara/Baixada and the Vale do Paraiba seems to form a single set. The Vale do Paraiba is the usual intergrading zone between Cotia and the former set. Santa Catarina and the Litoral is the third set, Bananal intermediate between it and the fourth set, Cotia/Campinas. Three localities, Terezopolis, Mangaratiba and Casimiro de Abreu are isolated.

4. Interorbital Constriction (Tables 4.37 and 4.38)

a. Coastal Transect - There is a break at Casimiro de Abreu, which is different from Ilheus but not from Guanabara. Mangaratiba is also linked with Guanabara and confirms the break between its set and the Litoral. This latter intergrades with Santa Catarina at Bananal.

b. Ilheus-Bananal Transect - The major samples along the transect are all different. However, the minor samples intergrade all major ones.

c. Litoral-Campinas Transect - All three localities are different between them.

d. Guanabara-Zona da Mata Transect - Terezopolis and Baixada

TABLE 4.37 INTERORBITAL EASTERN BRAZIL FEMALES BASIC STATISTICS

SAMP	N	MEAN	SDEV	SERR	CV	RANGE		AVSDEV		CONFL	
COTF	10	18.30	0.50	0.16	2.74	17.60	19.15	0.00	0.00	17.95	18.65
LITF	7	19.22	0.97	0.37	5.04	17.60	20.70	0.00	0.00	18.36	20.09
TERF	11	18.89	1.71	0.52	9.05	16.40	22.05	0.00	0.00	17.75	20.02
ZMMF	7	19.11	2.07	0.78	10.80	17.00	23.25	0.00	0.00	17.26	20.97
ILHF	5	19.46	0.94	0.42	4.83	18.20	20.70	0.00	0.00	18.38	20.54
BFLF	5	18.33	1.02	0.46	5.59	16.90	19.50	0.00	0.00	17.15	19.51
GBTF	5	19.48	0.80	0.36	4.10	18.25	20.15	0.00	0.00	18.56	20.40
SCAF	1	21.90	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
CAPF	2	20.18	0.00	0.00	0.00	18.50	21.85	0.00	0.00	0.00	0.00
BANF	2	18.98	0.00	0.00	0.00	17.45	20.50	0.00	0.00	0.00	0.00
VAPF	3	17.98	0.00	0.00	0.00	17.60	18.40	0.00	0.00	0.00	0.00
MNGF	1	21.95	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
CASF	1	22.55	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
ESPF	2	19.70	0.00	0.00	0.00	17.90	21.50	0.00	0.00	0.00	0.00

Table 4.38 - Females of Eastern Brazil. Levels of Probability of Significant Differences Betwee Samples. Interorbital Constriction.

Sample	p	SNK
Coastal Transect		
ILHF/Espf	.5	
ILHF/Casf	.05	break
GBTF/Casf	.3	
GBTF/Espf	.4	
GBTF/Mngf	.4	
BFLF/Casf	.01	break
BFLF/Mngf	.01	break
LITF/Mngf	.05	break
LITF/Banf	.6	
LITF/Scaf	.05	break
Ilheus-Bananal Transect		
Espf/ZMMF	.7	
ZMMF/Vapf	.9	
Vapf/COTF	.8	
COTF/Banf	.6	
Litoral-Campinas Transect		
LITF/COTF		break
COTF/Capf	.001	break

form a set which is different from both Zona da Mata and Guanabara.

e. Summary - This character has widely different coefficients of variability and no clear setting can be made from this mosaic of differentiations.

5. Postorbital Constriction (Table 4.39)

There is no break in the significant range of the Student-Newman Keuls test. Therefore the analysis was not carried out any further.

6. Breadth Across Canines (Table 4.40 and 4.41)

a. Coastal Transect - Ilheus and Espirito Santo form a set. Casimiro de Abreu and Guanabara are isolated one from the another and from the other samples. Baixada Fluminense is isolated in the transect as well. Litoral de Sao Paulo and Bananal can be lumped together, isolated from Santa Catarina.

b. Ilheus-Bananal Transect - This is a somewhat irregular transect, the extremes being different, but with Espirito Santo, there is significant differences from the Zona da Mata. But, it is the usual pattern for the rest, Vale do Paraiba as an intergrading zone between the extremes.

c. Litoral-Campinas Transect - The localities are all differentiated from one to another.

d. Guanabara - Zona da Mata Transect - Guanabara is isolated from the rest of the transect.

TABLE 4.39 POSTORBITAL EASTERN BRAZIL FEMALES BASIC STATISTICS

SAMP	N	MEAN	SDEV	SERR	CV	RANGE		AVSDEV		CONFL	
COTF	10	11.74	0.27	0.09	2.32	11.35	12.30	11.47	12.01	11.55	11.94
TERF	11	11.41	0.34	0.10	3.04	10.80	11.95	11.07	11.75	11.18	11.64
ZMMF	5	11.51	0.30	0.13	2.60	11.10	11.85	11.21	11.81	11.17	11.85
ILHF	5	11.44	0.70	0.31	6.04	10.75	12.20	10.74	12.14	10.65	12.23
BFLF	5	11.81	0.30	0.13	2.48	11.45	12.10	11.51	10.91	11.47	12.15
LITF	7	12.09	0.93	0.35	5.44	11.70	12.55	11.16	13.02	11.81	12.38
SCAF	2	11.45	0.00	0.00	0.00	11.20	11.70	0.00	0.00	0.00	0.00
BANF	2	11.50	0.00	0.00	0.00	11.60	11.40	0.00	0.00	0.00	0.00
CAPF	2	11.35	0.00	0.00	0.00	11.25	11.40	0.00	0.00	0.00	0.00
VAPF	3	11.22	0.00	0.00	0.00	10.90	11.55	0.00	0.00	0.00	0.00
MNGF	1	11.15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
CASF	1	11.80	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
ESPF	2	11.43	0.00	0.00	0.00	10.80	12.05	0.00	0.00	0.00	0.00
GBTF	50	11.18	0.48	0.21	4.28	10.55	11.70	10.70	11.66	10.63	11.73

TABLE 4.40. ACROSS CANINES EASTERN BRAZIL FEMALES BASIC STATISTICS

SAMP	N	MEAN	SDEV	SERR	CV	RANGE		AVSDEV		CONFL	
COTF	10	16.19	0.57	0.18	3.49	15.60	17.00	15.62	16.72	15.80	16.59
TERF	9	16.77	0.92	0.31	5.48	15.30	18.20	15.85	17.69	16.08	17.47
ZMMF	6	16.23	0.74	0.30	4.56	15.50	17.15	15.49	16.97	15.49	16.97
ILHF	5	18.17	1.53	0.68	8.40	16.25	19.90	16.64	19.70	16.41	19.93
BFLF	5	16.08	0.74	0.33	4.62	15.10	16.85	15.34	16.82	15.23	16.93
LITF	7	17.09	0.91	0.35	5.44	15.60	18.20	16.18	18.00	16.26	17.92
SCAF	1	18.90	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
BANF	2	16.20	0.00	0.00	0.00	16.10	16.30	0.00	0.00	0.00	0.00
CAPF	2	19.33	0.00	0.00	0.00	16.95	21.70	0.00	0.00	0.00	0.00
VAPF	3	16.23	0.00	0.00	0.00	15.10	16.90	0.00	0.00	0.00	0.00
MNGF	1	20.35	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
CASF	1	20.55	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
ESPF	2	18.50	0.00	0.00	0.00	17.20	19.80	0.00	0.00	0.00	0.00
GBTF	4	17.25	0.31	0.16	1.82	17.00	17.65	16.94	17.56	16.81	17.69

Table 4.41 - Females of Eastern Brazil. Levels of Probability of Significant Differences Between Samples. Across Canines.

Sample	p	SNK	
Coastal Transect			
ILHF/Espf	.3		
Casf/GBTF	.01		break
GBTF/Mngf	.01		break
BFLF/Casf	.001		break
BFLF/Mngf	.001		break
Mngf/LITF	.001		break
LITF/Banf	.3		break
LITF/Scaf	.001		break
Ilheus-Bananal Transect			
Espf/ZMMF	.01		break
ZMMF/Vapf	.2		
Vapf/COTF	.2		
COTF/Banf	.1		
Litoral-Lins Transect			
COTF/Capf	.001		break
LITF/COTF		*	break
Floresta da Tijuca-Zona da Mata Transect			
GBTF/BFLF		*	break
BFLF/TERF		NS	
TERF/ZMMF		NS	

e. Summary - The grouping suggested is: Ilheus, Espirito Santo, Zona da Mata, Terezopolis and Baixada Fluminense, intergrading with Cotia through the Vale do Paraiba; Guanabara, Mangaratiba, Casimiro de Abreu are isolated localities; Litoral is another set, together with Bananal; Cotia is isolated as well. There is a mosaic-like pattern in some areas for this character.

7. Breadth Across Molars (Tables 4.42 and 4.43)

a. Coastal Transect - Ilheus, Espirito Santo and Guanabara seems to be similar. The Baixada Fluminense is isolated. Guanabara and Litoral are together, the latter without differences with Bananal, but Santa Catarina is isolated.

b. Litoral-Campinas Transect - The three localities are different one to the other.

c. Guanabara - Zona da Mata Transect - The Baixada is isolated, the other localities belonging to the same set.

d. Summary - The degree of differentiation is low for this character. One actually could consider that, with the exception of the odd ones out (Baixada, Casimiro de Abreu and Mangaratiba), all localities belong to the same set. Cotia which is isolated integrates, however, through Bananal and Vale do Paraiba, with the other samples.

8. Breadth of the Palatal Shelf (Tables 4.44 and 4.45)

a. Coastal Transect - There is a break between Ilheus and Casimiro de Abreu. The Baixada intergrade with the northern localities,

TABLE 4.42 ACROSS MOLARS EASTERN BRAZIL FEMALES BASIC STATISTICS

SAMP	N	MEAN	SDEV	SERR	CV	RANGE		AVSDEV		CONFL	
COTF	10	29.01	0.67	0.21	2.32	27.90	30.00	29.68	28.34	28.54	29.49
TERF	9	29.67	1.08	0.36	3.66	28.25	31.00	30.75	28.59	28.85	30.49
ZMMF	6	28.78	1.09	0.43	3.62	26.90	29.90	29.87	27.69	27.74	29.82
ILHF	5	30.87	0.94	0.42	3.05	29.95	32.55	31.81	29.93	29.79	31.95
BFLF	4	28.51	0.71	0.36	2.51	27.65	29.10	29.22	27.80	27.52	29.50
LITF	7	30.06	0.54	0.20	1.80	29.10	30.65	30.60	29.52	29.57	30.54
SCAF	1	30.80	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
BANF	2	29.18	0.00	0.00	0.00	29.15	29.20	0.00	0.00	0.00	0.00
CAPF	3	28.48	0.00	0.00	0.00	27.90	29.10	0.00	0.00	0.00	0.00
VAPF	3	29.63	0.00	0.00	0.00	28.80	30.40	0.00	0.00	0.00	0.00
MNGF	1	33.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
CASF	1	29.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
ESPF	2	29.80	0.00	0.00	0.00	28.35	31.25	0.00	0.00	0.00	0.00
GBTF	5	29.69	0.46	0.21	1.56	29.10	30.20	29.23	30.15	29.16	30.22

Table 4.43 - Females of Eastern Brazil. Levels of Probability of Significant Differences Between Samples. Across Molars.

Sample	p	SNK	
Coastal Transect			
ILHF/Espf	.6		
ILHF/Casf	.05		break
Casf/GBTF	.01		break
GBTF/Mngf	.01		break
Casf/BFLF	.2		
Espf/BFLF	.05		break
BFLF/Mngf	.001		break
Mngf/LITF	.001		break
LITF/Banf	.3		
LITF/Scaf	.01		break
Ilheus-Bananal Transect			
Espf/ZMMF	.8		
ZMMF/Vapf	.9		
Vapf/COTF	.4		
COTF/Banf	.3		
Litoral-Campinas Transect			
LITF/COTF		*	break
COTF/Capf	.001		break
Floresta da Tijuca-Zona da Mata Transect			
GBTF/BFLF		*	break
BFLF/TERF		NS	
TERF/ZMMF		NS	

TABLE 4.44 PALATAL SHELF EASTERN BRAZIL FEMALES BASIC STATISTICS

SAMP	N	MEAN	SDEV	SERR	CV	RANGE		AVSDEV		CONFL	
COTF	9	17.19	0.61	0.21	3.66	16.55	18.55	16.58	17.80	16.71	17.66
TERF	10	17.18	1.38	0.46	8.04	15.40	19.80	15.80	18.56	16.12	18.24
ZMMF	4	16.80	1.07	0.53	6.36	15.40	18.00	15.73	17.87	15.32	18.28
ILHF	5	18.38	0.62	0.28	3.37	17.70	19.35	17.76	19.00	17.67	19.09
BFLF	5	16.90	1.09	0.49	6.45	15.70	18.00	15.81	17.99	15.65	18.15
LITF	7	17.71	0.79	0.30	4.43	16.60	18.55	16.92	18.50	17.01	18.42
SCAF	1	19.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
BANF	2	17.00	0.00	0.00	0.00	16.65	17.45	0.00	0.00	0.00	0.00
CAPF	2	17.98	0.00	0.00	0.00	17.60	18.35	0.00	0.00	0.00	0.00
VAPF	3	17.10	0.00	0.00	0.00	16.90	17.30	0.00	0.00	0.00	0.00
MNGF	1	19.65	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
CASF	1	16.60	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
ESPF	2	17.50	0.00	0.00	0.00	17.00	18.00	0.00	0.00	0.00	0.00
GBTF	4	18.22	0.68	0.34	3.74	17.55	18.90	17.54	18.90	17.28	19.17

Table 4.45 - Females of Eastern Brazil. Levels of Probability of Significant Differences Between Samples. Breadth of Palatal Shelf.

Sample	p	SNK
Coastal Transect		
ILHF/Espf	.4	
ILHF/Casf	.05	break
Espf/GBTF	.7	
Espf/BFLF	.7	
Casf/GBTF	.1	
GBTF/Mngf	.1	
Casf/BFLF	.3	
BFLF/Mngf	.05	break
Mngf/LITF	.05	break
LITF/Banf	.4	
LITF/Scaf	.2	
Ilheus-Bananal Transect		
Espf/ZMMF	.9	
ZMMF/Vapf	.7	
Vapf/COTF	.4	
COTF/Banf	.6	
Litoral-Campinas Transect		
LITF/COTF	*	break
COTF/Capf	.5	
Floresta da Tijuca-Zona da Mata Transect		
GBTF/BFLF	*	break
BFLF/TERF	*	break
TERF/ZMMF	NS	

being different from Ilheus, Guanabara and Mangaratiba.

Mangaratiba is intermediate between the litoral de Sao Paulo and Guanabara. Litoral forms a single set with Bananal and Santa Catarina.

b. Ilheus-Bananal Transect - The usual pattern, Cotia being different from Zona da Mata, but intergrading through Vale do Paraiba and linked with Bananal.

c. Litoral-Campinas Transect - Litoral de Sao Paulo significantly different from Cotia.

d. Guanabara-Zona da Mata Transect - Terezopolis is linked with the Zona da Mata and is different from Guanabara and Baixada Fluminense.

e. Summary - The grouping is the usual pattern: Ilheus, Espirito Santo, Zona da Mata, Terezopolis with the Vale do Paraiba as the intergrading zone with Cotia; the Rio de Janeiro litoral as usual, a mosaic; the litoral of Sao Paulo, Bananal and Santa Catarina another set, intergrading through the Bananal with Cotia.

9. Maxillary Toothrow (Table 4.46 and 4.47)

a. Coastal Transect - No differentiation accentuated but the somewhat usual confused area of Rio de Janeiro. Baixada Fluminense is isolated from all other samples in the State. Guanabara is different from the southern populations. Litoral, Bananal and Santa Catarina form a single set.

b. Ilheus-Bananal Transect - The usual pattern.

TABLE 4.46 MAXILLARY EASTERN BRAZIL FEMALES BASIC STATISTICS

SAMP	N	MEAN	SDEV	SERR	CV	RANGE		AVSDEV		CONFL	
COTF	9	39.58	1.00	0.33	2.51	38.35	40.75	38.58	40.58	38.83	40.33
TERF	8	40.00	2.15	0.76	5.38	37.30	44.25	37.85	42.15	38.20	41.80
ZMMF	6	39.96	0.79	0.32	1.97	38.90	40.95	39.17	40.75	39.17	40.75
ILHF	5	42.43	1.87	0.84	4.41	39.75	44.40	40.56	44.30	40.28	44.58
BFLF	5	38.94	0.47	0.21	1.20	38.45	39.55	38.47	39.41	38.40	39.48
LITF	7	40.99	1.48	0.56	3.62	38.50	42.85	39.51	42.47	39.67	42.32
SCAF	2	41.25	0.00	0.00	0.00	41.20	41.30	0.00	0.00	0.00	0.00
BANF	2	40.30	0.00	0.00	0.00	38.35	42.25	0.00	0.00	0.00	0.00
CAPF	2	40.40	0.00	0.00	0.00	39.30	41.50	0.00	0.00	0.00	0.00
VAPF	3	38.48	0.00	0.00	0.00	37.80	39.15	0.00	0.00	0.00	0.00
MNGF	1	41.15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
CASF	1	40.55	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
ESPF	2	39.28	0.00	0.00	0.00	39.25	39.30	0.00	0.00	0.00	0.00
GBTF	4	39.80	0.63	0.31	1.58	38.95	40.45	39.17	40.43	38.93	40.67

Table 4.47 - Females of Eastern Brazil. Levels of Probability of Significant Differences Between Samples. Maxillary Toothrow.

Sample	p	SNK
Coastal Transect		
ILHF/Espf	.2	
ILHF/Casf	.7	
GBTF/Casf	.3	
GBTF/Espf	.7	
GBTF/Mngf	.05	break
BFLF/Casf	.01	break
BFLF/Mngf	.01	break
Mngf/LITF	.3	
LITF/Banf	.6	
LITF/Scaf	.3	
Ilheus-Bananal Transect		
Espf/ZMMF	.4	
ZMMF/Vapf	.1	
Vapf/COTF	.6	
COTF/Banf	.7	
Litoral-Campinas Transect		
LITF/COTF	*	break
COTF/Capf	.9	
Floresta da Tijuca-Lins Transect		
GBTF/BFLF	*	break
BFLF/TERF	NS	
TERF/ZMMF	NS	

c. Litoral - Campinas Transect - Litoral is different from Cotia, that one belonging to the same set as Campinas.

d. Guanabara - Zona da Mata - Guanabara is different from the other samples in the transect.

e. Summary - The pattern is set as the points of a nippers (Guanabara and Baixada Fluminense) not touching, the joint being Ilheus. From Ilheus to Cotia, the usual intergrading at the Vale do Paraiba. Cotia intergrades with Litoral/Santa Catarina through Bananal, as usual.

10. Length of Upper Molar Series (Tables 4.48 and 4.49)

a. Coastal Transect - There is almost no differentiation in this transect, only the Baixada Fluminense having a significant difference with the other major samples.

b. Ilheus-Bananal Transect - Usual pattern, Cotia intergrading through the Vale do Paraiba with the rest of the transect.

c. Litoral-Campinas Transect - Litoral significantly different from the set Cotia/Campinas.

d. Guanabara-Zona da Mata Transect - Baixada Fluminense without links with any others in the transect. All others similar.

e. Summary - Low differentiation occurs in this character. Actually, only Cotia does not belong to the same set as the others, but it intergrades through the usual pattern. The Baixada Fluminense also intergrades with the others. It is better to say that there is almost homogeneity in the character through its distribution.

TABLE 4.48 MOLAR SERIES EASTERN BRAZIL FEMALES BASIC STATISTICS

SAMP	N	MEAN	SDEV	SERR	CV	RANGE		AVSDEV		CONFL	
COTF	9	18.61	0.54	0.18	2.91	18.00	19.40	18.07	19.15	18.20	19.02
LITF	7	19.10	0.71	0.27	3.74	18.20	20.30	18.39	19.81	18.46	19.74
TERF	9	18.43	0.82	0.27	4.47	17.35	20.05	17.61	19.25	17.80	19.07
ZMMF	7	18.61	0.74	0.28	3.98	17.85	20.60	17.87	19.35	17.97	19.29
ILHF	5	19.64	0.58	0.26	2.96	19.00	20.30	19.06	20.22	18.97	20.31
BFLF	5	18.45	0.65	0.29	3.52	17.50	19.10	17.80	19.10	17.70	19.20
GBTF	5	18.71	0.60	0.27	3.21	18.00	19.55	18.11	19.31	18.01	19.41
SCAF	2	19.65	0.00	0.00	0.00	19.60	19.70	0.00	0.00	0.00	0.00
BANF	2	18.44	0.00	0.00	0.00	18.05	18.85	0.00	0.00	0.00	0.00
CAPF	2	18.15	0.00	0.00	0.00	18.10	18.20	0.00	0.00	0.00	0.00
VAPF	3	18.48	0.00	0.00	0.00	18.10	18.85	0.00	0.00	0.00	0.00
MNGF	1	19.65	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
CASF	1	18.60	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
ESPF	2	18.68	0.00	0.00	0.00	18.50	18.85	0.00	0.00	0.00	0.00

Table 4.49 - Females of Eastern Brazil. Levels of Probability of Significant Differences Between Samples. Molar Series (Upper).

Sample	p	SNK
Coastal Transect		
ILHF/Espf	.2	
ILHF/Casf	.2	
GBTF/Casf	.4	
GBTF/Espf	.4	
GBTF/Mngf	.3	
BFLF/Casf	.4	
BFLFEspf	.6	
BFLF/Mngf	.2	
Mngf/LITF	.9	
LITF/Banf	.9	
LITF/Scaf	.9	
Ilheus-Bananal Transect		
Espf/ZMMF	.2	
ZMMF/Vapf	.3	
Vapf/COTF	.3	
COTF/Banf	.3	
Litoral-Campinas Transect		
LITF/COTF	*	break
COTF/Capf	.9	
Floresta da Tijuca-Zona da Mata Transect		
GBTF/BFLF	*	break
BFLF/TERF	*	break
TERF/ZMMF		NS

Breadth of Rostrum Across Jugals (Tables 4.50 and 4.51)

a. Coastal Transect - The transect goes up to Rio de Janeiro, where the usual mosaic pattern occurs, the Litoral, Bananal and Santa Catarina forming a single set.

b. Ilheus-Bananal Transect - Cotia, Bananal, Vale do Paraiba and Zona da Mata de Minas are a set seperated from Ilheus/Espirito Santo.

c. Litoral-Campinas Transect - Litoral de Sao Paulo is different from Cotia, which is different from Campinas.

d. Guanabara- Zona da Mata Transect - Baixada Fluminense and Terezopolis separated from the others.

e. Summary - The setting of localities set may be, Ilheus, Espirito Santo; Co ia, Zona da Mata and Terezopolis; and intermediate mosaic areas in Rio de Janeiro. Bananal intermediating Litoral/ Santa Catarina with Cotia.

12. Breadth of Rostrum Across Frontals (Table 4.52)

The result of the Student-Newman-Keuls shows no significant differences among the means of the major samples. No further study was made.

13. Length of Lower Molar Series (Tables 4.53 and 4.54)

a. Coastal Transect - There are two groupings, one from Ilheus to Casimiro de Abreu, the other from Guanabara to Santa Catarina. Baixada is out.

TABLE 4.50 ROSTRUM ACROSS JUGALS EASTERN BRAZIL FEMALES BASIC STATISTICS

SAMP	N	MEAN	SDEV	SERR	CV	RANGE		AVSDEV		CONFL	
COTF	9	24.31	0.89	0.30	3.66	22.85	25.65	23.42	25.20	23.64	24.96
TERF	10	24.34	2.11	0.70	8.68	21.45	28.25	22.22	26.45	22.79	25.88
ZMMF	7	23.65	1.25	0.47	5.31	21.35	25.50	22.40	24.90	22.53	24.77
ILHF	5	24.91	1.68	0.75	6.73	22.10	25.50	23.23	26.59	22.90	26.84
BFLF	5	23.37	1.07	0.48	4.58	21.85	24.55	22.30	24.44	22.14	24.60
LITF	7	25.09	2.10	0.80	8.39	21.05	26.50	22.99	27.19	23.20	26.97
SCAF	1	27.10	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
BANF	3	26.03	0.00	0.00	0.00	24.55	27.30	0.00	0.00	0.00	0.00
CAPF	2	26.53	0.00	0.00	0.00	25.15	27.90	0.00	0.00	0.00	0.00
VAPF	3	23.80	0.00	0.00	0.00	22.80	24.90	0.00	0.00	0.00	0.00
MNGF	1	27.20	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
CASF	1	28.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
ESPF	2	25.05	0.00	0.00	0.00	23.45	26.65	0.00	0.00	0.00	0.00
GBTF	5	26.28	1.16	0.52	4.43	24.60	27.45	25.64	27.96	24.92	27.62

Table 4.51 - Females of Eastern Brazil. Levels of Probability of Significant Differences Between Samples. Rostrum across Jugals.

Sample	p	SNK
Coastal Transect		
ILHF/Espf	.5	
ILHF/CASF	.2	
GBTF/Casf	.1	
GBTF/Espf	.7	
GBTF/Mngf	.9	
BFLF/Casf	.01	break
BFLF/Mngf	.01	break
Mngf/LITF	.7	
LITF/Banf	.7	
LITF/Scaf	.8	
Ilheus-Bananal Transect		
Espf/ZMMF	.02	break
ZMMF/Vapf	.5	
Vapf/COTF	.7	
COTF/Banf	.2	
Litoral-Campinas		
LITF/COTF	*	break
COTF/Capf	.02	break
Floresta da Tijuca-Zona da Mata Transect		
GBTF/BFLF	*	break
BFLF/TERF	NS	
TERF/ZMMF	*	break

b. Ilheus-Bananal Transect - Ilheus intergrades with Zona da Mata and Cotia through Espirito Santo. Cotia intergrades with Zona da Mata through Vale do Paraiba.

c. Litoral-Campinas Transect. - Usual pattern.

d. Guanabara - Zona da Mata Transect - All localities are different from each other.

e. Summary - Two major sets exist: Guanabara through Santa Catarina and Ilheus and Espirito Santo. Intergradation exists throughout the Paraiba Valley and Bananal, as usual. The intergrading mosaic still there in Rio de Janeiro State.

4.9 THE TRANSECTS II

4.9.1 Northern South America: Males

1. Greatest Length of Skull

a. Belem-San Nicolas Transect - There is no differentiation along this transect.

b. Santarem-Buenavista Transect - The Tapajos localities are fairly similar. Buenavista is with a higher level of probability.

c. Belem-Panama Transect - The higher significance is between Belem and Serra do Navio in this part of the transect. Intermediate localities have lower levels. Serra do Navio is significantly different from Surinam. All localities from Surinam to the west have low levels of significance, including Panama.

TABLE 4.52 ROSTRUM ACROSS FRONTALS EASTERN BRAZIL FEMALES BASIC STATISTICS

SAMP	N	MEAN	SDEV	SERR	CV	RANGE		AVSDEV		CONFL	
COTF	9	15.96	0.56	0.19	3.50	15.15	16.80	15.40	16.52	15.54	16.38
LITF	7	17.08	0.85	0.32	4.98	15.75	18.60	16.23	17.93	16.32	17.83
TERF	11	15.76	1.40	0.42	8.89	12.80	18.10	14.36	17.16	14.82	16.70
ZMMF	7	16.74	1.62	0.61	9.70	14.25	19.50	15.12	18.36	15.29	18.19
ILHF	5	16.33	0.87	0.39	5.32	14.95	17.05	15.46	17.20	15.33	17.33
BFLF	5	15.35	1.38	0.62	8.99	14.35	17.65	13.97	16.73	13.76	16.94
GBTF	5	16.96	1.55	0.69	9.11	15.00	18.40	15.41	18.51	15.18	18.74
SCAF	1	18.60	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
BANF	2	16.13	0.00	0.00	0.00	15.20	17.20	0.00	0.00	0.00	0.00
VAPF	3	15.78	0.00	0.00	0.00	14.90	16.15	0.00	0.00	0.00	0.00
MNGF	1	18.30	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
CASF	1	20.15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
ESPF	2	16.28	0.00	0.00	0.00	15.15	17.40	0.00	0.00	0.00	0.00
CAPF	2	18.23	0.00	0.00	0.00	16.80	19.65	0.00	0.00	0.00	0.00

TABLE 4.53 LENGTH OF SKULL NORTHERN SOUTH AMERICCA MALES BASIC STATISTICS

SAMP	N	MEAN	SDEV	SERR	CV	RANGE		AVSDEV		CONFL	
BELM	4	107.72	7.27	3.63	6.75	101.25	9.70	0.45	14.99	97.64	17.81
SENM	12	107.40	6.01	1.73	5.56	99.40	19.05	1.39	13.41	4.20	11.75
STMM	7	109.72	6.39	2.41	5.83	97.70	17.90	3.33	16.11	3.91	15.33
SURM	7	109.61	7.45	2.82	6.80	98.75	20.40	2.16	17.06	2.95	16.27
ARAM	1	98.40	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
BUEM	1	95.85	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
CAUM	3	100.50	0.00	0.00	0.00	97.90	4.95	0.00	0.00	0.00	0.00
CAXM	1	117.85	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
CHVM	1	113.40	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
COBM	1	101.10	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
CMTM	1	103.40	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
CURM	3	103.70	0.00	0.00	0.00	99.50	5.95	0.00	0.00	0.00	0.00
ESTM	1	97.15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
GUAM	2	105.03	0.00	0.00	0.00	101.15	8.90	0.00	0.00	0.00	0.00
KNKM	2	97.95	0.00	0.00	0.00	95.05	0.85	0.00	0.00	0.00	0.00
LUCM	1	120.90	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
MANM	1	101.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
MARM	1	99.80	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
MOTM	1	98.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
NEPM	2	107.63	0.00	0.00	0.00	94.55	20.70	0.00	0.00	0.00	0.00
PAUM	1	112.40	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
RIGM	1	113.40	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Table 4.54 - Males of Northern South America.Levels of Probability of Significant Differences Between Samples. Lenght of Skull.

Sample	p	SNK
Belem-Manaus Transect		
Belm/STMM	.7	
Cmtm/STMM	.8	
Curm/STMM	.8	
STMM/Paum	.8	
STMM/Manm	.5	
Santarem-Buenavista Transect		
STMM/Paum	.8	
STMM/Caxm	.5	
STMM/Buem	.1	
Belem-Panama Transect		
Belm/SENM	.2	
Curm/SENM	.7	
Chvm/SENM	.8	
SENM/SURM	*	break
SURM/Motm	.3	
SRUM/Marm	.4	
SURM/Nepm	.5	
SURM/PANM	.9	
Serra do Navio-Cobaria Transect		
SENM/Lucm	.02	break
Panama-Cauca Transect		
PANM/Caum	.5	
Pacific Coast Transect		
PANM/Guam	.8	
PANM/Riqm	.7	
Surinam-Manaus Transect		
SURM/Lucm	.3	
SURM/Knkm	.3	
SURM/Man	.6	
Panama-Buenavista Transect		
PANM/Cobm	.05	break

d. Serra do Navio-Cobaria Transect - Serra do Navio is significantly different from Lucie river. The transect breaks here.

e. Panama-Cauca Transect - No difference between the two localities.

f. Pacific Coast Transect - No differentiation.

g. Surinam-Manaus Transect - No differentiation along the transect.

h. Panama - Buenavista Transect - There is a break between Panama and Cobaria, interrupting the transect.

i. Summary - Serra do Navio is isolated from localities further West. However, it is integrated with the other samples through the Amazon mouth localities. A difference appears between the other localities and the ones at the foothill of the Andes, Cobaria, Amazonian Colombia and Buenavista, this latter being slightly different only from Santarem. A small differentiation appears between Serra do Navio and Belem.

2. Palatal Length (Table 4.54)

The SNK test showed no significant differences between the samples analysed. Therefore no further analysis was made.

3. Postorbital Constriction (Tables 4.55 and 4.56)

a. Belem-Manaus Transect - An homogeneous transect, without differentiation.

b. Santarem-Buenavista Transect - Transect without differentiation.

c. Belem-Panama Transect - The mouth of the Amazon localities

TABLE 4.55 PALATAL LENGHT NORTHERN SOUTH A MERICA MALES BASIC STATISTICS

SAMP	N	MEAN	SDEV	SERR	CV	RANGE		AVSDEV		CONFL	
BELM	4	63.13	3.29	1.65	5.22	58.90	66.85	59.84	66.42	58.56	67.69
SENM	11	62.87	2.43	0.73	3.83	59.85	67.15	60.44	65.30	61.26	64.48
STMM	9	63.81	2.70	0.90	4.23	59.40	68.38	61.11	66.51	61.78	65.85
SURM	7	62.69	3.30	1.25	5.26	57.45	67.10	59.39	65.99	59.74	65.63
ARAM	1	58.60	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
CAUM	3	63.40	0.00	0.00	0.00	62.05	64.33	0.00	0.00	0.00	0.00
CAXM	1	62.30	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
CHVM	1	67.15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
COBM	1	60.45	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
CURM	3	62.08	0.00	0.00	0.00	58.10	65.20	0.00	0.00	0.00	0.00
ESTM	1	58.40	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
GUAM	2	62.18	0.00	0.00	0.00	60.55	63.80	0.00	0.00	0.00	0.00
KNKM	2	61.25	0.00	0.00	0.00	58.70	60.60	0.00	0.00	0.00	0.00
LUCM	1	63.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
MANM	1	61.65	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
MARM	1	61.60	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
MOTM	1	58.75	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
NEPM	2	65.05	0.00	0.00	0.00	59.55	70.55	0.00	0.00	0.00	0.00
RIOM	1	61.60	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
TRIM	1	58.75	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Table 4.56 - Males of Northern South America.Levels of Probability of Significant Differences Between Samples. Postorbital.

Sample	p	SNK
Belem-Manaus Transect		
Belm/STMM	.9	
Cmtm/STMM	.9	
Curm/STMM	.8	
STMM/Paum	.9	
STMM/Itcm	.5	
STMM/Manm	.9	
Santarem-Buenavista Transect		
STMM/Paum	.9	
STMM/Caxm	.9	
STMM/Buem	.6	
Belem-Panama Transect		
Belm/SENM	.9	
Curm/SENM	.5	
SENM/SURM	*	break
SURM/Trim	.01	break
PANM/Nepm	.2	
PANM/Marm	.8	
PANM/Motm	.2	
PANM/Trim	.01	
Serra do Navio-Cobaria Transect		
SENM/Lucm	.4	
SENM/Knkm	.2	
SENM/Aram	.6	
SENM/Cobm	.9	
Panama-Cauca Transect		
PANM/Caum	.7	
Pacific Coast Transect		
PANM/Guam	.6	
PANM/Riqm	.9	

Table 4.56 (continuation)

Surinam-Manaus Transect	
SURM/Lucm	.2
SURM/Knkm	.4
SURM/Manm	.1
Panama-Buenavista Transect	
PANM/Aram	.5
PANM/Cobm	.4
PANM/Buem	.3

and Serra do Navio show no differences. There is a break between Serra do Navio and Surinam and between Surinam and Trinidad. Then the transect was analysed from west to east: Panama shows no differences with Sao Juan Nepomuceno, Santa Marta and Motopan; there is a break between Panama and Trinidad.

d. Serra do Navio-Cobaria Transect - No differentiation along the transect. Notice that the localities further way have lower probabilities values.

e. Panama-Cauca Transect - No differences.

f. Pacific Coast Transect - No differences can be found.

g. Surinam-Manaus Transect - Transect without differentiation.

h. Panama - Buenavista Transect - Low levels of significance, no differentiation seems to occur.

i. Summary - The following grouping can be suggested: Panama, San Juan Nepomuceno, Santa Marta and Motopan; Trinidad; Surinam; Serra do Navio and Mouth of Amazon. The whole of Amazonia shows no differentiation with the samples I have, all sets above may considered to be intergraded with the others. Cauca and the Pacific Coast again are linked with Panama.

4. Breadth Across Molars (Table 4.57 and 4.58)

a. Belem Manaus Transect - The localities nearer the major samples of Santarem have lower levels of probable difference than the ones at the mouth of the Amazon and Manaus. But no differentiation can be pinpointed.

TABLE 4.57 ACROSS MOLARS NORTHERN SOUTH AMERICA MALES BASIC STATISTICS

SAMP	N	MEAN	SDEV	SERR	CV	RANGE		AVSDEV		CONFL	
BELM	4	29.77	1.60	0.80	5.38	27.85	31.35	28.17	31.37	27.55	32.00
SENM	12	30.90	1.05	0.30	3.40	29.45	33.55	29.85	31.95	30.24	31.56
STMM	8	30.22	1.67	0.60	5.52	27.75	32.65	28.55	31.89	28.86	31.58
SURM	6	30.95	1.41	0.58	4.57	29.05	30.85	29.54	26.72	29.54	32.36
ARAM	1	29.30	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
BUEM	1	29.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
CAUM	3	31.50	0.00	0.00	0.00	30.25	33.20	0.00	0.00	0.00	0.00
CHVM	1	30.75	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
COBM	1	31.90	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
CMTM	1	31.10	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
CURM	2	30.60	0.00	0.00	0.00	29.55	31.65	0.00	0.00	0.00	0.00
CAXM	1	28.40	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
ESTM	1	30.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
GUAM	3	30.07	0.00	0.00	0.00	29.60	30.35	0.00	0.00	0.00	0.00
ITCM	1	28.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
KNKM	2	29.20	0.00	0.00	0.00	28.80	29.60	0.00	0.00	0.00	0.00
LUCM	1	31.80	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
MANM	1	30.90	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
PAUM	1	28.40	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
RIOM	1	30.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
TRIM	1	29.55	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Table 4.58-Males of Northern Brazil.Levels of Probability of Significant Differences Between Samples. Across Molars.

Sample	p	SNK
Belem-Manaus Transect		
Belm-STMM	.6	
Cmtm/STMM	.7	
Curm/STMM	.5	
STMM/Panm	.9	
STMM/Itcm	.9	
STMM/Manm	.6	
Santarem-Buenavista Transect		
STMM/Paum	.9	
STMM/Caxm	.9	
STMM/Buem	.7	
Belem-Panama Transect		
Belm/SENM	.7	
Curm/SENM	.7	
Chvm/SENM	.6	
SENM/SURM		NS
SURM/Tri	.8	
SURM/PANM	.9	
Serra do Navio-Cobaria Transect		
SENM/Lucm	.9	
SENM/Knkm	.3	
SENM/Aram	.4	
SENM/Cobm	.8	
Pacific Coast Transect		
PANM/Guam	.7	
PANM/Riqm	.9	
Surinam-Manaus Transect		
SURM/Lucm	.7	

(continued)

Table 4.58 (continuation)

Surinam-Manaus (continuation)	
SURM/Knlm	.5
SURM/Manm	.3
Panama-Buenavista Transect	
PANM/Cobm	.6
PANM/Aram	.4
PANM/Buem	.4

b. Santarem-Buenavista Transect - No differentiation.

c. Belem-Panama Transect - A homogeneous transect from Belem to Panama.

d. Serra do Navio-Coabaria Transect - No differentiation.

e. Panama-Cauca Transect - No significant differences found, low level of probability.

f. Pacific Coast Transect - No differentiation.

g. Surinam-Manaus Transect - No differences found. However, the level of probability is high between Manaus and Surinam.

h. Panama-Buenavista Transect - No differentiation appears from the data I have studied.

i. Summary - There is no apparent differentiation in this character. The only significant difference is between Surinam and Santarem, (Fig. 4.17). However, all intermediate samples intergrades these two. Notice that Manaus, the closest to Santarem to be compared with Surinam had a higher probability value of significance than the average for the character as a whole.

5. Breadth of Brain Case (Tables 4.59 and 4.60)

a. Belem-Manaus Transect - No differentiation in this transect, with very low levels of probability.

b. Santarem-Buenavista Transect - No differences were found.

c. Belem-Panama Transect - Serra do Navio significantly different from Chaves. Surinam significantly different from both Serra do

TABLE 4.59 BRAIN CASE NORTHERN SOUTH AMERICA MALES BASIC STATISTICS

SAMP	N	MEAN	SDEV	SERR	CV	RANGE		AVSDEV		CONFL	
BELM	4	29.77	0.79	0.40	2.89	28.48	30.06	26.20	28.10	26.12	28.30
SENM	2	29.55	1.13	0.33	3.83	28.42	30.60	28.35	31.85	28.84	30.26
STMM	9	28.29	2.05	0.68	7.26	26.24	30.34	23.45	30.75	26.75	29.84
SURM	5	29.93	0.80	0.36	2.67	29.13	30.73	28.75	30.85	29.01	30.85
ARAM	1	26.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
BUEM	1	29.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
CAUM	3	28.43	0.00	0.00	0.00	0.00	0.00	27.95	28.75	0.00	0.00
CAXM	1	26.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
CHVM	1	26.60	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
COBM	1	27.95	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
CMTM	1	26.80	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
CURM	2	26.90	0.00	0.00	0.00	0.00	0.00	25.25	28.55	0.00	0.00
ESTM	1	27.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
GUAM	2	29.28	0.00	0.00	0.00	0.00	0.00	29.05	29.50	0.00	0.00
ITCM	1	26.40	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
KNKM	2	25.28	0.00	0.00	0.00	0.00	0.00	24.35	26.20	0.00	0.00
LUCM	1	26.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
MANM	1	25.30	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
MARM	1	29.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
MOTM	1	24.65	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
NEPM	2	29.68	0.00	0.00	0.00	25.75	31.70	0.00	0.00	0.00	0.00
PAUM	1	26.95	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
RIOM	1	30.85	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Table 4.60 - Males of Northern South America.Levels of Probability of Significant Differences Between Samples. Breadth Brain Case.

Sample	p	SNK
Belem-Manaus Transect		
STMM/Curm	.9	
STMM/Cmtm	.9	
STMM/Belm	.9	
STMM/Paum	.9	
STMM/Itcm	.9	
STMM/Manm	.4	
Santarem-Buenavista Transect		
STMM/Paum	.9	
STMM/Caxm	.8	
STMM/Buem	.7	
Belem-Panama Transect		
SENM/Chvm	.02	break
SENM/SURM	*	break
SURM/Manm	.001	break
PANM/Nepm	.01	break
Serra do Navio-Cobaria Transect		
SENM/Lucm	.001	break
Panama-Cauca Transect		
PANM/Caum	.5	
Pacific Coast Transect		
PANM/Guam	.05	break
Surinam-Manaus Transect		
SURM/Lucm	.001	break
Panama-Buenavista Transect		
PANM/Nepm	.01	break

Navio and Santa Marta. Panama significantly different from San Juan Nepomuceno. Notice that all differences by the t test were highly significant.

d. Serra do Navio-Cobaria Transect - A highly significant break between Serra do Navio and Lucie River.

e. Panama-Cauca Transect - No difference found

f. Pacific Coast Transect - Significant difference between Panama and Guayaquil.

g. Surinam-Manaus Transect - Highly significant difference between Lucie River and Surinam.

h. Panama-Buenavista Transect - Very significant difference between Panama and San Juan Nepomuceno.

i. Summary - The following sets can be constructed: All samples South of the Amazon River, including Itacoatiara and Manaus in the north bank. Serra do Navio; Surinam; Panama and Cauca; Guayaquil and Rique. Several minor samples were not tested against major ones. Surinam has no significant difference with Santarem.

6. Breadth of Palatal Shelf (Table 4.61)

No significant differences found between the major samples. No analysis was made.

7. Length of Upper Molar Series (Table 4.62 and 4.63)

a. Belem-Manaus Transect - Very low levels of significance along

TABLE 4.61 PALATAL SHELF NORTHERN SOUTH AMERICA MALES BASIC STATISTICS

SAMP	N	MEAN	SDEV	SERR	CV	RANGE		AVSDEV		CONFL	
BELM	4	16.14	1.43	0.72	8.83	14.71	17.57	15.00	18.05	14.14	18.14
SENM	11	17.80	0.98	0.30	5.50	16.82	18.78	16.40	19.30	17.15	18.45
STMM	7	17.44	1.01	0.38	5.82	16.43	18.45	15.70	18.50	16.53	18.34
SURM	6	16.83	1.37	0.56	8.13	15.46	18.20	14.80	18.85	15.47	18.20
ARAM	1	16.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
BUEM	1	17.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
CAUM	3	16.75	0.00	0.00	0.00	15.65	18.45	0.00	0.00	0.00	0.00
CAXM	1	16.20	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
CHVM	1	17.20	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
COBM	1	16.40	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
CURM	2	16.10	0.00	0.00	0.00	15.10	17.00	0.00	0.00	0.00	0.00
ESTM	1	27.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
GUAM	2	17.20	0.00	0.00	0.00	16.60	17.80	0.00	0.00	0.00	0.00
KNKM	2	16.88	0.00	0.00	0.00	16.50	17.25	0.00	0.00	0.00	0.00
LUCM	1	17.45	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
MANM	1	18.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
MARM	1	17.95	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
NEPM	1	16.55	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
PANM	7	17.57	0.71	0.27	4.05	16.55	18.70	0.00	0.00	16.94	18.20

TABLE 4.62 MOLAR SERIES NORTHERN SOUTH AMERICA MALES BASIC STATISTICS

SAMP	N	MEAN	SDEV	SERR	CV	RANGE		AVSDEV		CONFL	
BELM	3	19.03	0.00	0.00	0.00	18.40	19.70	0.00	0.00	0.00	0.00
PANM	5	20.37	1.09	0.49	5.36	18.80	21.40	19.28	21.46	19.12	21.62
SENM	12	19.88	0.63	0.18	4.57	18.85	21.00	19.25	20.51	19.48	20.74
STMM	8	19.41	0.59	0.21	3.04	18.60	20.45	18.82	20.00	18.92	19.89
SURM	8	19.08	0.57	0.20	2.97	17.90	19.45	18.51	19.65	18.62	19.54
ARAM	1	18.30	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
BUEM	1	18.90	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
CAUM	3	19.10	0.00	0.00	0.00	19.05	19.15	0.00	0.00	0.00	0.00
CAXM	1	20.45	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
CHVM	1	21.15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
COBM	1	19.35	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
CMTM	1	20.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
CURM	3	18.82	0.00	0.00	0.00	18.15	19.65	0.00	0.00	0.00	0.00
ESTM	1	18.85	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
GUAM	3	19.00	0.00	0.00	0.00	18.50	19.30	0.00	0.00	0.00	0.00
ITCM	1	18.95	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
KNKM	2	18.70	0.00	0.00	0.00	18.60	18.80	0.00	0.00	0.00	0.00
LUCM	0	19.35	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
MANM	1	19.15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
MARM	1	18.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
NEPM	2	19.78	0.00	0.00	0.00	18.75	20.80	0.00	0.00	0.00	0.00
PAUM	1	19.55	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
SONM	1	19.30	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
TRIM	1	19.30	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Table 4.63-Males of Northern South America.Levels of Probability of Significant Differences Between Samples. Upper Molar Series.

Sample	p	SNK
Belem-Manaus Transect		
STMM/Cntm	.9	
STMM/Belm	.8	
STMM/Paum	.5	
STMM/Itcm	.9	
STMM/Manm	.9	
Santarem-Buenavista Transect		
STMM/Paum	.5	
STMM/Caxm	.4	
STMM/Buenm	.9	
Belem-Panama Transect		
SENM/Chvm	.4	
SENM/Belm	.6	
SENM/SURM	*	break
SURM/Trim	.7	
SURM/Marm	.5	
SURM/Nepm	.7	
SURM/PANM	.02	
PANM/Nepm	.9	
PANM/Marm	.9	
PANM/Trim	.9	
Serra do Navio-Cobaria Transect		
SENM/Lucm	.9	
SENM/Knkm	.1	
SENM/Aram	.02	break

(continued)

Table 4.63 (continuation)

Panama-Cauca Transect	
PANM/Sonm	.5
PANM/Caum	.4
Pacific Coast Transect	
PANM/Guam	.3
Surinam-Manaus Transect	
SURM/Lucm	.7
SURM/Knkm	.9
SURM/Manm	.4
Panama-Buenavista Transect	
PANM/Nepm	.8
PANM/Cobm	.5
PANM/Buem	.3

the transect.

b. Santarem-Buenavista Transect - No differentiation in the transect.

c. Belem-Panama Transect - From Belem to Serra do Navio, no differentiation. There is a break between Serra do Navio and Surinam. From Surinam to Sao Juan Nepomuceno there is again no differentiation. However, there is a significant difference between Surinam and Panama. They intergrade in the intermediate populations, but it must be noticed that the levels of porbability are somewhat lower from West to East.

d. Serra do Navio-Cobaria Transect - There is a break between Arauca River and Serra do Navio.

e. Panama-Cauca Transect - No differentiation found.

f. Pacific Coast - No differentiation.

g. Surinam-Manaus Transect - No differentiation.

h. Summary - Localities South and along the Amazon River show no differentiation. They intergrade with Serra do Navio through the localities in the mouth of the River and they intergrade belonging to the same set with Surinam. That locality is different from Panama, however for the whole of the region there is intergradation between these two localities.

8. Greatest Breadth of Nasals (Tables 4.65 and 4.66)

a. Belem-Manaus Transect - No differentiation, as usual. Lower

TABLE 4.65 NASAL BREADTH NORTHERN SOUTH AMERICA MALES BASIC STATISTICS

SAMP	N	MEAN	SDEV	SERR	CV	RANGE		AVSDEV		CONFL	
BELM	4	15.36	1.44	0.72	9.39	13.25	16.40	13.92	16.80	13.36	17.36
PANM	8	15.34	2.52	0.89	16.44	11.80	19.55	12.82	17.86	13.29	17.39
SENM	11	15.65	1.03	0.31	6.60	13.80	16.55	14.62	16.68	14.96	16.33
STMM	9	16.21	1.80	0.60	11.13	13.90	19.85	14.41	18.01	14.85	17.56
SURM	6	15.73	0.87	0.35	5.51	14.25	16.55	14.86	16.60	14.86	16.59
ARAM	1	14.80	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
BUEM	1	14.40	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
CAUM	3	16.20	0.00	0.00	0.00	14.75	16.95	0.00	0.00	0.00	0.00
CAXM	1	15.80	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
CHVM	1	17.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
COBM	1	15.75	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
CMTM	1	13.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
CURM	2	14.20	0.00	0.00	0.00	13.95	14.45	0.00	0.00	0.00	0.00
ESTM	1	15.85	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
GUAM	3	16.33	0.00	0.00	0.00	16.20	16.55	0.00	0.00	0.00	0.00
ITCM	1	14.80	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
KNKM	2	16.25	0.00	0.00	0.00	13.60	18.90	0.00	0.00	0.00	0.00
LUCM	1	17.60	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
MANM	1	15.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
MARM	1	14.30	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
MOTM	1	16.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
NEPM	2	17.35	0.00	0.00	0.00	16.95	17.75	0.00	0.00	0.00	0.00
PAUM	1	16.95	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
RIGM	1	17.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
SONM	1	15.30	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
TRIM	1	14.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Table 4.66-Males of Northern South America.Levels of Probability.
Greatest Breadth of Nasals.

Belem-Manaus Transect*	
STMM/Curm	.6
STMM/Cmtm	.3
STMM/Belm	.8
STMM/Paum	.7
STMM/Itcm	.9
STMM/Manm	.9
Santarem-Buenavista Transect	
STMM/Paum	.7
STMM/Caxm	.5
STMM/Buem	.7
Belem-Panama Transect	
SENM/Chvm	.2
SENM/Curm	.3
SENM/Belm	.3
SENM/SURM	* break
SURM/Trim	.2
SURM/Motm	.5
SURM/Nepm	.2
SURM/PANM	.8
Serra do Navio Cobaria Transect	
SENM/Lucm	.1
SENM/Knkm	.7
SENM/Aram	.9
SENM/Cobm	.3
Panama-Cauca Transect	
PANM/Sonm	.9
PANM/Caum	.8

Table 4.66 (continuation)

Pacific Coast Transect	
PANM/Guam	.8
PANM/Riqm	.4
Surinam-Manaus Transect	
SURM/Lucm	.1
SUR/Knkm	.9
SURM/Manm	.9
Panama-Buenavista Transect	
PANM/Nepm	.5
PANM/Cobm	.9
PANM/Aram	.9
PANM/Buem	.8

values of probability between the samples around Santarem.

b. Santarem-Buenavista Transect - Only the usual break between Serra do Navio and Surinam.

c. Serra do Navio-Cobaria Transect - No differences were found to be significant.

d. Panama-Cauca Transect - Very similar samples revealed by the test.

e. Pacific Coast Transect - No differences. Notice that the further locality has lower similarity.

f. Surinam-Manaus Transect - Again no differences were found.

g. Panama-Buenavista Transect - No significant differences were found.

h. Summary - There is no high degree of differentiation in this highly variable intralocal character. Only Serra do Navio is different from Surinam, but again, Serra do Navio is not isolated.

9. Length of Nasals (Table 4.68 and 4.69)

a. Belem-Manaus Transect - There are two breaks in the transect, Santarem with Chaves and Santarem with Itacoatiara, both on the North bank of the Amazon.

b. Santarem-Buenavista Transect - There is a very significant difference between Santarem and Buenavista.

c. Belem-Panama Transect - There is no differences between Serra do Navio and the localities in the Mouth of the Amazon. The usual

TABLE 4.68 LENGHT OF NASALS NORTHERN SOUTH AMERICA MALES BASIC STATISTICS

SAMP	N	MEAN	SDEV	SERR	CV	RANGE		AVSDEV		CONFL	
BELM	3	52.05	0.00	0.00	0.00	50.20	53.30	0.00	0.00	0.00	0.00
SENM	10	50.47	3.39	1.07	6.72	44.40	55.55	47.07	53.86	48.07	52.86
STMM	9	52.14	2.29	0.76	4.39	47.85	55.80	49.85	54.43	50.42	53.87
SURM	8	51.67	4.08	1.44	7.90	57.90	47.10	47.59	55.75	48.34	55.01
ARAM	1	43.95	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
BUEM	1	43.30	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
CAUM	3	44.82	0.00	0.00	0.00	43.85	46.10	0.00	0.00	0.00	0.00
CAXM	1	49.10	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
CHVM	1	55.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
COBM	1	46.10	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
CMTM	1	47.30	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
CURM	3	50.65	0.00	0.00	0.00	50.10	51.20	0.00	0.00	0.00	0.00
GUAM	3	49.53	0.00	0.00	0.00	45.60	52.85	0.00	0.00	0.00	0.00
KNKM	2	47.50	0.00	0.00	0.00	45.30	49.70	0.00	0.00	0.00	0.00
ITCM	1	43.85	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
LUCM	1	54.55	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
MANM	1	47.95	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
MARM	1	47.10	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
NEPM	2	49.98	0.00	0.00	0.00	42.45	57.50	0.00	0.00	0.00	0.00
PAUM	1	52.60	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
RIOM	1	57.60	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
SONM	1	50.80	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
TRIM	1	48.30	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Table 4.69-Males of Northern South America.Levels of Probability. Lenght of Nasals.

Sample	p	SNK
Belem-Manaus Transect		
STMM/Curm	.9	
STMM/Chvm	.02	break
STMM/Belm	.3	
STMM/Paum	.4	
STMM/Itcm	.01	break
Santarem-Buenavista Transect		
STMM/Paum	.4	
STMM/Caxm	.5	
STMM/Buem	.01	break
Belem-Panama Transect		
SENM/Curm	.3	
SENM/Chvm	.3	
SENM/Belm	.6	
SENM/SURM		break
SURM/Trim	.9	
SURM/Manm	.6	
SURM/Nepm	.3	
Serra do Navio Transect		
SENM/Lucm	.5	
SENM/Knkm	.9	
SENM/Aram	.1	
SENM/Cobm	.5	
Surinam-Manaus Transact		
SURM/Lucm	.7	
SURM/Knkm	.8	
SURM/Manm	.9	

break between Surinam and Serra do Navio is present. From Surinam to the West there is a diminishing level of probability or, in other words, an apparent increase of similarity from east to west.

d. Serra do Navio-Cobaria Transect - No differences were found.

e. Surinam-Manaus Transect - No differences were found.

f. Summary - Buenavista seems isolated from the Northern localities. Localities around Santarem are not different from Belem, but Santarem is similar to Surinam and Surinam is different from Serra do Navio. The mosaic here is incomplete because Gardner (1973) from whom I got the Panamanian statistics did not measure this character.

10. Length of Lower Molar Series (Tables 4.70 and 4.71)

a. Belem-Manaus Transect - No differences were found, very low probabilities between Santarem and all other localities.

b. Santarem-Buenavista Transect - No differences were found.

c. Santarem-Panama Transect - Serra do Navio is isolated from Chaves and Surinam. No significant differences along the transect farther west, but the level of probability of significance of difference between Surinam and Panama is somewhat high.

d. Serra do Navio-Cobaria - No differences between Serra do Navio and Lucie River, but a significant difference between the former and Kanuku Mountains.

e. Panama-Cauca Transect - Very low values of significance in this transect.

TABLE 4.70 LOWER MOLAR SERIES NORTHERN SOUTH AMERICA MALES BASIC STATISTICS

SAMP	N	MEAN	SDEV	SERR	CV	RANGE		AVSDEV		CONFL	
BELM	4	22.03	0.63	0.31	2.84	21.30	22.80	21.40	22.66	21.60	22.46
SENM	12	22.87	0.69	0.20	3.03	21.60	23.70	22.18	23.56	22.43	23.30
STMM	8	22.20	0.71	0.25	3.18	21.50	23.75	21.49	22.91	21.62	22.78
SURM	7	21.70	0.95	0.36	4.36	21.50	23.75	20.75	22.65	20.86	22.54
PANM	9	22.42	0.67	0.22	3.01	21.10	23.60	21.75	23.09	21.91	22.93
ARAM	1	21.90	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
BUEM	1	21.75	0.00	0.00	0.00	21.30	22.20	0.00	0.00	0.00	0.00
CAUM	3	22.27	0.00	0.00	0.00	21.35	22.75	0.00	0.00	0.00	0.00
CAXM	1	22.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
CHVM	1	24.35	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
COBM	1	21.60	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
CMTM	1	22.85	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
CURM	3	21.82	0.00	0.00	0.00	21.05	23.05	0.00	0.00	0.00	0.00
ESTM	1	21.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
GUAM	3	21.38	0.00	0.00	0.00	21.00	21.60	0.00	0.00	0.00	0.00
ITCM	1	21.35	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
KNKM	2	21.48	0.00	0.00	0.00	21.40	21.55	0.00	0.00	0.00	0.00
LUCM	1	21.75	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
MANM	1	21.70	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
MARM	1	21.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
MOTM	1	20.55	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
NEPM	2	22.20	0.00	0.00	0.00	21.45	22.95	0.00	0.00	0.00	0.00
PAUM	1	22.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
SONM	1	22.20	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
TRIM	1	21.85	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Table 4.71-Males of Northern South America.Levels of Probability. Lenght of Lower Molar Series.

A

Sample	p	SNK
Transect Belem-Manaus		
STMM/Curm	.9	
STMM/Cmtm	.8	
STMM/Belm	.6	
STMM/Paum	.7	
STMM/Itcm	.5	
STMM/Manm	.9	
Santarem-Buenavista Transect		
STMM/Paum	.7	
STMM/Caxm	.7	
STMM/Buem	.9	
Belem-Panama Transect		
SENM/Chvm	.05	break
SENM/SURM	*	break
SURM/Trim	.2	
SURM/Motm	.2	
SURM/Marm	.3	
SURM/Nepm	.6	
SURM/PANM	.1	
Serra do Navio-Cobaria Transect		
SENM/Lucm	.2	
SENM/Knkm	.05	break
Panama-Cauca Transect		
PANM/Sonm	.8	
PANM/Caum	.9	

(continued)

Table 4.71 - (continuation)

Pacific Coast Transect	
PANM/Guam	.2
Surinam-Manaus Transect	
SURM/Lucm	.9
SURM/Knkm	.9
SURM/Manm	.9
Panama-Buenavista Transect	
PANM/Nepm	.8
PANM/Cobm	.3
PANM/Aram	.5
PANM/Buem	.3

f. Pacific Coast Transect - No significant differences.

g. Pacific Coast Transect - No significant difference.

h. Surinam-Manaus Transect - No differences found.

i. Panama-Buenavista Transect - No differences found.

j. Summary - It can be said that only Serra do Navio is isolated.

4.9.2 Northern South America: Females

1. Zygomatic Breadth (Tables 4.73 and 4.73)

a. Belem-San Nicolas Transect - Belem and Curralinho has no significant differences. Santarem is different from both Caldeirao and Belem but has no significant differences with Manaus and San Nicolas.

b. Belem-Panama Transect - Belem, Curalinho and Mexiana have no differences, the latter and Belem are significantly different from Serra do Navio. Surinam is not different from Serra do Navio and has no differences with the localities further west. The same applies from Panama to the East, Panama and Surinam being significantly different.

c. Serra do Navio-Cobaria Transect - No differences.

d. Panama-Cauca Transect - No differences were found.

e. Surinam-San Nicolas Transect - No differences

f. Panama-San Nicolas Transect - No differences found.

TABLE 4.72 ZYGOMATIC NORTHERN SOUTH AMERICA FEMALES BASIC STATISTICS

SAMP	N	MEAN	SDEV	SERR	CV	RANGE		AVSDEV		CONFL	
BELF	6	49.49	3.23	1.32	6.53	44.90	53.05	46.26	52.72	46.26	52.72
CALF	6	48.32	3.11	1.27	6.44	42.70	51.25	45.21	51.43	45.21	51.43
CAUF	3	51.82	0.00	0.00	0.00	49.70	54.25	0.00	0.00	0.00	0.00
CURF	13	51.87	4.04	1.12	7.79	45.70	60.55	47.83	55.91	49.44	54.29
SENF	13	52.27	1.80	0.50	3.45	49.60	54.80	50.47	54.07	51.19	53.35
STMF	4	49.68	0.00	0.00	0.00	46.50	56.50	0.00	0.00	0.00	0.00
SURF	6	54.71	4.57	1.86	8.35	47.60	59.70	50.14	59.28	50.15	59.27
ARAF	1	47.90	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
MANF	2	50.40	0.00	0.00	0.00	41.60	59.20	0.00	0.00	0.00	0.00
COBF	3	52.90	0.00	0.00	0.00	47.90	59.00	0.00	0.00	0.00	0.00
HUAF	1	48.20	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
KASF	1	49.10	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
MEXF	2	47.75	0.00	0.00	0.00	47.35	48.15	0.00	0.00	0.00	0.00
SNIF	1	50.75	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
SONF	1	49.20	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
URAF	2	51.05	0.00	0.00	0.00	50.60	51.50	0.00	0.00	0.00	0.00
PANF	12	49.54	3.72	1.07	7.73	44.20	57.15	45.82	53.26	47.18	51.90

Table 4.73-Females Northern South America.Levels of Probability. Zygomatic Breadth.

Sample	p	SNK	
Belem-San Nicolas Transect			
BELF/CURF		NS	
BELF/CALF		*	break
STMF/CURF		*	break
STMF/Manf	.4		
STMF/Snif	.5		
Belem-Panama Transect			
BELF/CURF		NS	
BELF/Mexf	.6		
BELF/SENF		*	break
SENF/Mexf	.02		break
SENF/SURF		NS	
SURF/Argf	.3		
SURF/Kasf	.5		
SURF/Uraf	.9		
SURF/PANF	.001		break
PANF/Uraf	.8		
PANF/Kasf	.9		
PANF/Argf	.7		
Serra do Navio-Cobaria Transect			
PANF/Cobf	.4		
Panama-Cauca Transect			
PANF/Uraf	.8		
PANF/CAUF	.6		
Surinam-San Nicolas Transect			
SURF/Manf	.8		
SURF/Snif	.9		
Panama-San Nicolas Transect			
PANF/Uraf	.8		
PANF/Cobf	.5		
PANF/Snif	.8		

g. Summary - The following setting can be made: Belem and Curralinho; Sera do Navio, Surinam intergrading with Panama to the west and with Santarem and associates in the south.

2. Interorbital Constriction

a. Belem-San Nicolas Transect - Belem and Curralinho with significant differences with Caldeirao and Santarem, which are similar. No differences farther West.

b. Belem-Panama Transect - Belem, Curralinho and Mexiana separated from Caldeirao and Serra do Navio. That one is different from Surinam. The usual intergradation of Panama through Surinam, with the extremes different.

c. Serra do Navio- Pamplona Transect - No differences found.

d. Panama-Cauca Transect - A significant difference was found between Cauca and Panama.

e. Surinam-San Nicolas Transect - No differences.

f. Panama-San Nicolas Transect - No differences.

g. Summary - The following grouping can be suggested: Belem, Curralinho and Mexiana; Serra do Navio; Surinam intergrading; Panama and the other localities is west; Cauca Valley. Serra do Navio intergrades with Santarem through Caldeirao and Santarem intergrades with the other, through Manaus and San Nicolas.

3. Postorbital Constriction (Tables 4.76 and 4.77)

a. Belem-San Nicolas Transect - The only break is between Santarem

TABLE 4.74 INTERORBITAL NORTHERN SOUTH AMERICA FEMALES BASIC STATISTICS

SAMP	N	MEAN	SDEV	SERR	CV	RANGE		AVSDEV		CONFL	
BELF	6	19.77	0.87	0.36	7.52	18.25	20.70	18.90	20.64	18.90	20.65
CALF	4	18.34	0.00	0.00	0.00	14.30	19.90	0.00	0.00	0.00	0.00
CAUF	4	21.86	0.00	0.00	0.00	20.55	23.95	0.00	0.00	0.00	0.00
CURF	13	20.08	1.47	0.41	7.30	0.00	0.00	18.61	21.55	19.20	20.96
PANF	9	19.08	1.66	0.00	8.70	17.00	22.60	17.42	20.74	0.00	0.00
SENF	13	20.94	1.22	0.34	5.84	19.30	22.60	19.72	22.16	20.21	21.67
STMF	6	21.41	1.40	0.57	6.53	19.65	23.30	20.01	22.81	19.94	22.87
SURF	7	21.18	2.07	0.78	9.77	18.15	23.65	19.11	23.25	19.32	23.03
MANF	2	20.03	0.00	0.00	0.00	17.15	22.90	0.00	0.00	0.00	0.00
COBF	2	19.85	0.00	0.00	0.00	18.00	20.70	0.00	0.00	0.00	0.00
HUAF	1	18.70	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
KASF	1	19.55	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
MEXF	2	18.13	0.00	0.00	0.00	17.80	18.45	0.00	0.00	0.00	0.00
PAMF	1	20.55	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
SNIF	1	19.90	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
SONF	2	22.00	0.00	0.00	0.00	20.60	23.40	0.00	0.00	0.00	0.00
URAF	2	20.50	0.00	0.00	0.00	19.70	21.30	0.00	0.00	0.00	0.00

Table 4.75- Females Northern South America. Levels of Probability. Interorbital Constriction.

Sample	p	SNK	
Belem-San Nicolas Transect			
BELF/CURF		NS	
BELF/Calf	.05		break
STMM/Calf	.2		
STMM/CURF		*	break
STMM/Manf	.7		
STMM/Snif	.7		
Belem-Panama Transect			
BELF/CURF		NS	
BELF/Calf	.05		break
BELF/Mexf	.2		
SENF/Mexf	.01		break
SENF/CALF.	.2		
SENF/SURF		*	break
SURF/Kasf	.9		
SURF/Uraf	.4		
SURF/PANF	.05		break
PANF/Uraf	.5		
PANF/Kasf	.8		
Serra do Navio-Pamplona Transect			
SENF/Cobf	.8		
SENF/Pamf	.5		
Panama-Cauca Transect			
PANF/Uraf	.5		
PANF/CAUF	.05		break
Surinam-San Nicolas Transect			
SURF/Manf	.6		
SURF/Snif	.7		
Panama-San Nicolas Transect			
PANF/Uraf	.5		
PANF/Pamf	.5		
PANF/Snif	.7		

TABLE 4.76 POSTORBITAL NORTHERN SOUTH AMERICA FEMALES BASIC STATISTICS

SAMP	N	MEAN	SDEV	SERR	CV	RANGE		AVSDEV		CONFL	
BELF	6	11.43	0.76	0.31	6.62	10.40	12.35	10.67	12.19	10.68	12.19
CALF	6	10.93	0.42	0.17	3.82	10.50	11.50	10.51	11.35	10.52	11.35
CAUF	5	11.61	0.37	0.17	3.19	11.05	12.00	11.24	11.98	11.15	12.07
CURF	13	11.18	0.64	0.18	5.73	10.20	12.80	10.54	11.78	10.79	11.56
SENF	13	12.17	0.82	0.23	6.71	11.10	14.40	11.35	12.99	11.68	12.66
STMF	5	11.26	0.40	0.18	8.80	10.85	11.90	10.86	11.66	10.76	11.76
SURF	7	12.00	0.74	0.28	6.14	11.05	13.10	11.26	12.64	11.34	12.66
PANF	10	11.49	0.38	0.12	3.34	11.00	12.20	11.11	11.87	11.22	11.76
ARAF	1	11.85	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
MANF	2	10.88	0.00	0.00	0.00	10.35	11.40	0.00	0.00	0.00	0.00
COBF	3	12.12	0.00	0.00	0.00	11.85	12.60	0.00	0.00	0.00	0.00
HUAF	1	12.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
KASF	1	11.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
MEXF	2	10.95	0.00	0.00	0.00	10.85	11.05	0.00	0.00	0.00	0.00
PAMF	1	12.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
SNIF	1	12.20	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
SONF	2	11.58	0.00	0.00	0.00	11.55	11.60	0.00	0.00	0.00	0.00
URAF	2	11.53	0.00	0.00	0.00	10.80	12.25	0.00	0.00	0.00	0.00

Table 4.77-Females Northern South America.Levels of Probability. Postorbital Constriction.

Sample	p	SNK	
Belem-San Nicolas Transect			
BELF/CURF		NS	
BELF/CALF		NS	
BELF/STMF		NS	
STMF/Manf	.3		
STMF/Snif	.001		break
Belem-Panama Transect			
BELF/CURF		NS	
BELF/CALF		NS	
BELF/SENF		NS	
SENF/SURF		*	break
SURF/Argf	.1		
SURF/Kasf	.1		
SURF/Uraf	.7		
SURF/PANF	.2		
Serra do Navio-Pamplona Transect			
SENF/Pamf	.4		
Panama-Cauca Transect			
PANF/Sonf	.9		
PANF/Cauf	.1		
Surinam-San Nicolas Transect			
SURF/Manf	.3		
SURF/Snif	.5		
Panama-San Nicolas Transect			
PANF/Uraf	.7		
PANF/Snif	.4		

and San Nicolas.

b. Belem-Panama Transect - The only break is between Surinam and Serra do Navio.

c. Serra do Navio-Pamplona Transect - No difference.

d. Panama-Cauca Transect - No difference, but lower level of similarity between the extremes.

e. Surinam-San Nicolas Transect - No differences were found.

f. Panama-San Nicolas Transect - Without differences.

g. Summary - Very low differentiation occurs in this character. The interesting point is the usual differences between Serra do Navio and Surinam and the result of Surinam being different from all other samples. However both samples intergrades with all other ones through intermediate localities.

4. Breadth Across Canines (Tables 4.78 and 4.79)

a. Belem-San Nicolas Transect - No differentiation is apparent in this transect.

b. Belem-Panama Transect - The only significant difference is between Surinam and Panama, as usual.

c. Serra do Navio-Pamplona Transect - Significant difference exists between Pamplona and Serra do Navio.

d. Panama-Cauca Transect - Panama has a break with Sonson and that one has no significant difference with Cauca.

TABLE 4.78 ACORSS CANINES NORTHERN SOUTH AMERICA FEMALES BASIC STATISTICS

SAMP	N	MEAN	SDEV	SERR	CV	RANGE		AVSDEV		CONFL	
BELF	6	17.76	0.72	0.30	4.08	16.70	18.75	17.04	18.48	17.03	18.48
CALF	5	17.00	1.47	0.66	8.66	14.60	18.40	15.53	18.47	15.30	18.70
CAUF	6	19.20	0.70	0.29	3.66	18.15	19.95	18.50	19.90	18.46	19.94
CURF	12	18.72	1.33	0.38	7.09	17.00	20.45	17.39	19.05	17.89	19.66
PANF	10	17.38	0.77	0.24	4.43	16.10	19.20	16.61	18.15	16.83	17.93
SENF	13	19.02	0.58	0.16	3.04	18.15	20.35	18.44	19.60	18.67	19.36
STMF	4	17.95	0.00	0.00	0.00	17.30	19.30	0.00	0.00	0.00	0.00
SURF	7	18.93	1.90	0.72	10.05	16.70	21.70	17.03	20.83	17.23	20.63
ARAF	1	17.15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
MANF	2	17.38	0.00	0.00	0.00	14.85	19.90	0.00	0.00	0.00	0.00
COBF	3	18.23	0.00	0.00	0.00	17.15	20.15	0.00	0.00	0.00	0.00
HUAF	1	18.15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
KASF	1	19.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
MEXF	2	16.73	0.00	0.00	0.00	16.50	16.95	0.00	0.00	0.00	0.00
PAMF	1	17.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
SNIF	1	18.70	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
SONF	2	19.60	0.00	0.00	0.00	17.55	21.65	0.00	0.00	0.00	0.00
URAF	2	17.33	0.00	0.00	0.00	17.05	17.60	0.00	0.00	0.00	0.00

Table 4.79-Females of Northern South America.Levels of Probability. Breadth Across Canines.

Sample	p	SNK
Belem-San Nicolas Transect		
BELF/CALF		NS
BELF/CURF		NS
BELF/STMF	.7	
STMF/Manf	.9	
STMF/Snif	.9	
Belem-Panama Transect		
BELF/CALF		NS
BELF/CURF		NS
BELF/SENF		NS
SENF/SURF		NS
SURF/Argf	.9	
SURF/Kasf	.2	
SURF/Uraf	.9	
SURF/PANF	.05	break
Serra do Navio-Pamplona Transect		
SENF/Pamf	.01	break
Panama-Cauca Transect		
PANF/Sonf	.05	break
CAUF/Sonf	.2	
Surinam-San Nicolas Transect		
SURF/Manf	.9	
SURF/Snif	.2	
Surinam-San Nicolas Transect		
SURF/Manf	.9	
SURF/Snif	.2	
Panama-San Nicolas Transect		
PANF/Uraf	.9	
PANF/Pamf	.7	
PANF/Cobf	.4	
PANF/Snif	.2	

e. Surinam-San Nicolas Transect - Surinam is quite similar to Manaus, but has a higher level of probability with San Nicolas, tough without being a significant one.

f. Panama-San Nicolas Transect - The probabilities, all not significant increase with distances, and, with the exception of Pamplona there is a increase in the average value of the character.

g. Summary - This character appears to be very homogeneous, the differences found can be interpreted as being due to the distance between the samples, since higher probabilities appear in this way, not all of them significant ones.

5. Breadth of Brain Case (Tables 4.80 and 4.81)

a. Belem-San Nicolas Transect - The Mouth of the Amazon localities have a break with Santarem. Santarem has no significant differences with Manaus and San Nicolas.

b. Belem-Panama Transect - Mexiana has no differences with Belem and Serra do Navio. It is intermediate between the localities in the mouth of the Amazon and Serra do Navio. Surinam is isolated from Serra do Navio and from Aragua.

Panama has no significant differences with the localities farther east, but with Aragua, it has a higher probability.

c. Serra do Navio-Cobaria - No difference.

d. Panama-Cauca Transect - Panama has a significant difference with Cauca but it seems that they intergrade in the intermediate

TABLE 4.80 BRAIN CASE NORTHERN SOUTH AMERICA FEMALES BASIC STATISTICS

SAMP	N	MEAN	SDEV	SERR	CV	RANGE		AVSDEV		CONFL	
BELF	6	26.12	0.59	1.45	5.57	23.80	28.00	25.53	26.71	24.66	27.57
CALF	5	24.89	1.78	0.80	7.15	21.90	26.65	23.11	26.67	22.84	26.94
CAUF	5	27.96	1.93	0.86	6.91	25.45	29.90	26.03	29.89	25.56	30.36
CURF	13	27.29	0.60	0.60	7.97	22.75	30.85	26.69	27.89	25.99	28.59
PANF	9	26.52	2.25	0.75	8.50	23.60	30.50	24.27	28.77	24.79	28.25
SENF	10	27.64	1.58	0.50	5.71	26.10	30.50	26.06	29.22	26.53	28.76
STMF	6	27.03	2.00	0.85	7.71	24.90	30.55	24.95	29.11	24.84	29.21
SURF	7	28.04	1.86	0.70	6.65	25.55	30.20	26.18	29.90	26.38	29.71
ARAF	1	20.95	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
MANF	2	26.48	0.00	0.00	0.00	0.00	0.00	22.30	30.65	0.00	0.00
COBF	3	25.50	0.00	0.00	0.00	0.00	0.00	20.95	29.40	0.00	0.00
HUAF	1	30.45	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
KASF	1	28.85	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
MEXF	2	25.40	0.00	0.00	0.00	0.00	0.00	24.85	25.95	0.00	0.00
SNIF	1	26.80	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
SONF	2	28.35	0.00	0.00	0.00	26.30	30.40	0.00	0.00	0.00	0.00
URAF	2	26.45	0.00	0.00	0.00	25.35	27.55	0.00	0.00	0.00	0.00

Table 4.01 -Females Northern South America. Levels of Probability. Breadth of Brain Case.

Belem-San Nicolas Transect			
BELF/CALF		NS	
BELF/CURF		NS	
BELF/STMF		*	break
STMF/Manf	.5		
STMF/Snif	.4		
Belem-Panama Transect			
BELF/CALF		NS	
BELF/CURF		NS	
BELF/Mexf	.8		
BELF/SENF		*	break
SENF/Mexf	.3		
SENF/SURF		*	break
SURF/Argf	.001		
PANF/Uraf	.9		
PANF/Kasf	.4		
PANF/Argf	.1		
Serra do Navio-Cobaria Transect			
SENF/Cobf	.4		
Panama-Cauca Transect			
PANF/Uraf	.9		
PANF/SOnf	.5		
PANF/CAUF	.01		break
CAUF/Sonf	.2		
Surinam-San Nicolas Transect			
SURF/Manf	.9		
SURF/Snif	.8		
Panama-Buenavista Transect			
PANF/Uraf	.9		
PANF/Cobf	.8		
PANF/Snif	.9		

localities.

e. Surinam-San Nicolas Transect - No differentiation in this transect.

f. Panama-San Nicolas Transect - No differentiation is again apparent in this transect.

g. Summary - The following grouping can be suggested: Belem, Caldeirao and Curralinho; Serra do Navio; Surinam; Panama and North Venezuela localities; Cauca; and Santarem. San Nicolas and Manaus and intermediate between Surinam and Santarem and between Panama and Santarem. Sonson intergrades Panama with Cauca.

6. Breadth of Palatal Shelf (Tables 4.82 and 4.83).

a. Belem-San Nicolas Transect - Belem and Curralinho have a significant difference between them. Curralinho has no differences between Curralinho and Santarem. Caleirao has no difference with the other samples. Santarem has a significant difference with Manaus.

b. Belem-Panama Transect - There is a break between Serra do Navio and Belem. Serra do Navio has no differences with Caldeirao and Curralinho. Surinam has the usual level of significant differeneces with Serra do Navio. There is no significant difference with any localities to the West.

c. Serra do Navio-Cobaria Transect - No difference found

d. Panama-Cauca Transect - No significant difference was found in the transect.

TABLE 4.82 PALATAL SHELF NORTHERN SOUTH AMERICA FEMALES BASIC STATISTICS

SAMP	N	MEAN	SDEV	SERR	CV	RANGE		AVSDEV		CONFL	
BELF.	5	17.45	1.00	0.45	5.72	16.10	18.40	0.00	0.00	16.30	18.60
CALF	4	15.80	0.00	0.00	0.00	14.70	17.00	0.00	0.00	0.00	0.00
CAUF	6	17.74	0.49	0.20	2.75	16.85	18.25	17.25	18.23	17.23	18.25
CURF	11	17.82	0.91	0.27	5.11	16.90	20.15	16.91	18.73	17.21	18.42
PANF	12	17.74	0.85	0.25	4.82	16.40	18.75	16.89	18.59	17.19	18.29
SENF	8	18.17	0.82	0.29	4.50	16.70	19.15	17.35	18.99	17.51	18.84
STMF	10	17.15	1.55	0.69	9.05	15.65	19.15	15.60	18.70	15.22	19.08
SURF	7	17.96	1.58	0.60	8.79	15.80	19.70	16.38	19.54	16.55	19.37
ARAF	1	17.80	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
MANF	1	13.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
COBF	2	18.60	0.00	0.00	0.00	17.80	19.40	0.00	0.00	0.00	0.00
HUAF	1	17.20	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
KASF	1	16.75	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
SNIF	1	18.15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
SONF	1	19.20	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
URAF	1	18.45	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Table 4.83-Females Northern South America.Levels of Probability. Breadth of Palatal Shelf.

Sample	p	SNF	
Belem-San Nicolas Transect			
BELF/CURF		*	break
CALF/CURF	.3		
STMF/BELF		*	break
STMF/CALF	.5		
STMF/CURF		NS	
STMF/Manf	.02		break
Belem- Panama Transect			
BELF/CURF		*	break
BELF/CALF	.3		
BELF/SENF		*	break
SENF/CALF	.1		
SENF/CURF		NS	
SENF/SURF		*	break
SURF/Argf	.3		
SURF/Kasf	.9		
SURF/Uraf	.4		
SURF/PANF	.7		
Serra do Navio-Cobaria Transect			
SENF/Cobf	.8		
Panama-Cauca Transect			
PANF/Uraf	.5		
PANF/Sonf	.2		
PANF/CAUF	.9		
Surinam-San Nicolas Transect			
SURF/Manf	.01		break
Panama-San Nicolas Transect			
PANF/Uraf	.5		
PANF/Cobf	.4		
PANF/Snif	.7		

e. Surinam-San Nicolas Transect - There is a break in the transec between Surinam and Manaus.

f. Panama-San Nicolas Transect - There is no significant differentiation in the transect.

g. Summary - The pattern of the sets is the usual: Belem isolated; Serra do Navio and Santarem in this case with Curralinho in the same set; Surinam throughout North Venezuela, to Panama and Cauca; Manaus isolated. The intergrading zone is more confused in this case.

7. Length of Maxillary Toothrow (Tables 4.84 and 4.85)

a. Belem-San Nicolas Transect - Belem is isolated. The same applies to Caldeirao. Curralinho belongs to the same set as Santarem together with Manaus and San Nicolas.

b. Belem-Panama Transect - No difference can be found between Mexiana and Belem since they have the same mean. Belem, except for Mexiana, is isolated. Serra Navio is isolated except for Curralinho. Surinam is different from Aragua and Panama is different from Uraba.

c. Serra do Navio-Cobaria Transect - No differences were found

d. Surinam-San Nicolas Transect - There is a break in the transect between Surinam and Manaus.

e. Panama-San Nicolas Transect - The above-mentioned break between Panama and Uraba.

f. Panama-Cauca Transect - Panama is isolated and Cauca has a

TABLE 4.84 MAXILLARY NORTHERN SOUTH AMERICA FEMALES BASIC STATISTICS

SAMP	N	MEAN	SDEV	SERR	CV	RANGE		AVSDEV		CONFL	
BELF	6	40.90	1.16	0.47	2.83	39.05	42.35	39.74	42.06	39.74	42.06
CALF	6	39.75	1.44	0.59	3.63	37.70	41.30	38.31	41.19	38.31	41.19
CAUF	6	41.72	1.16	0.47	2.77	40.15	42.85	40.56	42.87	40.50	42.93
CURF	10	41.76	1.56	0.49	3.73	39.55	44.30	40.20	43.32	40.66	42.86
PANF	9	41.47	0.64	0.21	1.53	40.60	42.25	40.83	42.11	40.98	41.96
SENF	13	41.29	1.16	0.32	2.80	39.05	42.85	40.13	42.45	40.60	41.98
STMF	5	40.91	1.05	0.47	2.57	39.50	42.40	39.86	41.96	39.60	42.22
SURF	7	42.04	1.42	0.54	3.38	40.50	43.70	40.62	43.46	40.77	43.30
ARAF	1	37.75	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
MANF	2	38.98	0.00	0.00	0.00	35.05	42.90	0.00	0.00	0.00	0.00
SCRF	1	38.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
COBF	3	40.07	0.00	0.00	0.00	37.75	42.00	0.00	0.00	0.00	0.00
CUMF	1	38.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
HUAF	1	41.80	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
KASF	1	38.90	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
MEXF	1	41.75	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
SNIF	1	41.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
SONF	2	39.85	0.00	0.00	0.00	38.90	40.80	0.00	0.00	0.00	0.00
URAF	2	43.25	0.00	0.00	0.00	42.55	43.95	0.00	0.00	0.00	0.00

Table 4.85-Females Northern South America. Levels of Probality. Maxillary Toothrow.

Sample	p	SNK	
Belem-San Nicolas Transact			
BELF/CALF		*	break
BELF/CURF		*	break
STMF/CALF		*	break
STMF/CURF		NS	
STMF/Manf	.2		
STMF/Snif	.5		
Belem-Panama Transect			
BELF/CURF		*	break
BELF/CALF		*	break
BELF/Mexf	.000		
SENF/CALF		*	break
SENF/CURF		NS	
SENF/Mexf	.4		
SENF/SURF		*	break
SURF/Argf	.01		break
PANF/Uraf	.05		break
Serra do Navio-Cobaria Transect			
SENF/Cobf	.9		
Panama-Cauca Transect			
PANF/Uraf	.05		break
PANF/Sonf	.001		break
Surinam-San Nicolas Transect			
SURF/Manf	.01		
Panama-San Nicolas Transect			
PANF/Uraf	.05		break

highly significant difference with Sonson.

g. Summary - There several significant differences among the samples in this character. The following sets can be suggested: Belem; Caldeirao; Surinam; North Venezuela and Colombia; Panama; Cauca; Santarem, Manaus and San Nicolas. Intergrading occurs through Curralinho between Serra do Navio and Santarem. Mexiana has no difference with Serra do Navio but has the highly improbable one hundred percent possibility of belonging to Belem.

8. Length of Upper Molar Series (Tables 4.86 and 4.87)

a. Belem-San Nicolas Transect - Santarem has significant differences with the localities in the Mouth of the Amazon. No differences were found between Santarem and Manaus and San Nicolas.

b. Belem-Panama Transect - Serra do Navio is isolated. Surinam belongs to the same set of Kasmera and Uraba. Panama has a significant difference with Uraba.

c. Serra do Navio-Cobaria Transect - No difference was found.

d. Panama-Cauca Transect - Both Panama and Cauca are isolated by breaks in the transect.

e. Surinam-San Nicolas Transect - No differences were found. Only the probability is higher for the extreme localities compared.

f. Panama-San Nicolas Transect - Panama is isolated.

g. Summary - The following sets can be suggested: Mouth of Amazon; Serra do Navio; Surinam and Northern Colombia and Venezuela;

TABLE 4.86 MOLAR SERIES NORTHERN SOUTH AMERICA FEMALES BASIC STATISTICS

SAMP	N	MEAN	SDEV	SERR	CV	RANGE		AVSDEV		CONFL	
BELF	6	19.14	0.60	0.47	3.14	18.15	19.70	18.64	19.74	39.74	42.05
CALF	6	18.94	0.56	0.23	2.92	18.00	19.55	18.38	19.50	18.39	19.49
CAUF	6	19.65	0.46	0.19	2.35	19.10	20.45	19.19	20.11	19.16	20.14
CURF	9	19.31	0.27	0.09	1.41	19.00	19.90	19.04	19.58	19.10	19.51
PANF	12	21.80	0.44	0.13	2.03	21.15	22.60	21.36	22.24	21.52	22.08
SENF	13	19.53	0.31	0.15	2.86	18.70	20.50	19.22	19.84	19.19	19.86
STMF	6	19.17	0.41	0.17	2.16	18.75	19.85	18.40	19.50	18.73	19.60
SURF	7	19.61	1.20	0.45	6.10	18.20	21.85	18.41	20.81	18.54	20.68
ARAF	1	18.15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
MANF	1	18.70	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
SCRF	1	18.30	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
COBF	3	19.00	0.00	0.00	0.00	18.15	19.55	0.00	0.00	0.00	0.00
CUMF	1	18.30	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
HUAF	1	19.90	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
KASF	1	17.70	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
MEXF	1	18.75	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
SNIF	1	19.20	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
SONF	2	18.38	0.00	0.00	0.00	18.15	18.60	0.00	0.00	0.00	0.00
URAF	2	20.35	0.00	0.00	0.00	20.30	20.40	0.00	0.00	0.00	0.00

Table 4.87-Females Northern South America.Levels of Probability. Lenght of Upper Molar Series.

Sample	p	SNK	
Belem-San Nicolas Transect			
BELF/CURF		NS	
BELF/CALF		NS	
BELF/STMF		*	break
STMF/Manf	.6		
STMF/SNIF	.4		
Belem-Panama Transect			
BELF/CURF		NS	
BELF/CALF		NS	
BELF/Mexf	.9		
BELF/SENF		*	break
SENF/SURF		*	break
SURF/Argf	.5		
SURF/Kasf	.3		
SURF/Uraf	.9		
PANF/SURF	.01		break
PANF/Uraf	.01		break
Serra do Navio-Cobaria Transect			
SENF/Cobf	.5		
Surinam-San Nicolas Transect			
SURF/Manf	.9		
SURF/Snif	.5		
Panama-San Nicolas Transect			
PANF/Uraf	.01		break

Panama; Cauca; Uaraba and Sonson; Santarem, Manaus and San Nicolas. There is intergrading of Surinam and Santarem through the last two localities.

9. Breadth of Rostrum Across Jugals (Table 4.88)

The Student-Newman-Keuls test carried out among the major samples found no significance in the differences of the means. Therefore, no further analyses was carried out.

10. Length of Nasals (Tables 4.89 and 4.90)

a. Belem-San Nicolas Transect - No difference was found significant along the transect.

b. Belem-Panama Transect - No difference was found significant.

c. Serra do Navio-Pamplona Transect - No difference was found significant.

d. Cauca Valley Transect - No difference was found significant.

e. Surinam-San Nicolas Transect - No difference was found significant.

f. Summary - This character is homogeneous throughout its distribution. The only significant difference is between Cauca and the other Major samples.

11. Length of Lower Molar Series (Table 4.91 and 4.92)

a. Belem-San Nicolas Transect - Belem is isolated. Santarem has

TABLE 4.88 ROSTRUM ACROSS JUGALS NORTHERN SOUTH AMERICA FEMALES BASIC STATIST

SAMP	N	MEAN	SDEV	SERR	CV	RANGE		AVSDEV		CONFL	
BELF	6	26.88	0.88	0.36	3.27	25.70	27.70	26.88	27.76	26.01	27.76
CALF	4	26.00	0.00	0.00	0.00	21.90	29.30	0.00	0.00	0.00	0.00
CAUF	5	29.08	1.04	0.47	3.61	0.00	0.00	28.03	30.13	27.78	30.38
CURF	13	28.05	1.23	0.34	4.40	25.35	29.70	26.82	29.28	27.31	29.79
PANF	9	26.07	2.03	0.68	7.77	22.75	30.30	24.04	28.10	24.51	27.63
SENF	13	28.97	1.25	0.35	4.32	27.30	31.50	27.72	30.22	28.22	29.72
STMF	4	26.90	0.00	0.00	0.00	25.60	29.05	0.00	0.00	0.00	0.00
SURF	6	29.33	1.64	0.67	5.60	27.60	31.80	27.69	30.97	27.69	30.97
ARAF	1	25.55	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
MANF	2	27.13	0.00	0.00	0.00	24.20	30.05	0.00	0.00	0.00	0.00
COBF	3	26.37	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
HUAF	1	26.35	0.00	0.00	0.00	24.75	28.80	0.00	0.00	0.00	0.00
KASF	1	25.55	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
MEXF	2	26.28	0.00	0.00	0.00	25.10	27.45	0.00	0.00	0.00	0.00
PAMF	1	25.80	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
SNIF	1	26.75	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
SONF	2	28.45	0.00	0.00	0.00	25.65	31.25	0.00	0.00	0.00	0.00
URAF	2	25.33	0.00	0.00	0.00	25.00	25.65	0.00	0.00	0.00	0.00

TABLE 4.89 NASAL LENGHT NORTHERN SOUTH AMERICA FEMALES BASIC STATISTICS

SAMP	N	MEAN	SDEV	SERR	CV	RANGE		AVSDEV		CONFL	
BELF	4	49.99	0.00	0.00	0.00	47.10	53.40	0.00	0.00	0.00	0.00
CALF	4	44.61	0.00	0.00	0.00	42.90	45.50	0.00	0.00	0.00	0.00
CAUF	5	45.82	3.53	1.58	7.71	43.20	49.25	42.29	49.35	41.43	50.21
CURF	12	49.15	4.52	1.30	9.19	42.00	55.35	44.63	53.67	46.30	51.99
SENF	12	48.42	2.89	0.84	8.64	43.55	54.10	45.53	51.31	46.60	50.24
STMF	5	48.47	3.65	1.63	7.54	44.10	53.95	44.82	52.12	43.93	53.01
SURF	7	50.32	3.23	1.22	6.43	45.15	56.15	47.09	53.55	47.43	53.21
ARAF	1	43.65	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
MANF	1	54.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
SCRF	1	42.10	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
COBF	2	42.70	0.00	0.00	0.00	41.75	43.65	0.00	0.00	0.00	0.00
CUMF	1	42.10	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
HUAF	1	44.55	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
KASF	1	45.15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
MEXF	2	44.10	0.00	0.00	0.00	40.10	48.10	0.00	0.00	0.00	0.00
PAMF	1	46.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
SNIF	1	49.95	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
SONF	2	46.03	0.00	0.00	0.00	44.05	48.00	0.00	0.00	0.00	0.00
URAF	2	48.38	0.00	0.00	0.00	46.35	50.40	0.00	0.00	0.00	0.00

Table 4.90-Females Northern South America. Levels of Probability. Lenght of Nasals.

Sample	p	SNK
Belem-San Nicolas Transect		
BELF/CURF	.3	
BELF/CALF	.1	
BELF/STMF	.7	
STMF/Manf	.3	
STMF/Snif	.5	
Belem-Panama Transect		
BELF/CURF		NS
BELF/CALF	.1	
BELF/Mexf	.2	
BELF/SENF	.8	
SENF/SURF		NS
SURF/Scrf	.1	
SURF/Argf	.2	
SURF/Kasf	.3	
SURF/Uraf	.9	
Serra do Navio-Pamplona Transect		
SENF/Cobf	.1	
SENF/Pamf	.9	
Cauca Valley Transect		
CAUF/Sonf	.2	
CAUF/Uraf	.8	
Surinam-San Nicolas Transect		
SURF/Manf	.6	
SURF/Snif	.6	

TABLE 4.91 LOWER MOLAR SERIES NORTHERN SOUTH AMERICA BASIC STATISTICS

SAMP	N	MEAN	SDEV	SERR	CV	RANGE		AVSDEV		CONFL	
BELF	6	21.94	0.76	0.31	3.48	20.95	23.05	21.18	22.70	21.19	22.70
CALF	5	21.30	0.53	0.24	2.50	20.70	21.90	20.77	21.30	20.70	21.92
CAUF	6	22.13	0.69	0.28	3.13	21.00	22.75	21.43	22.82	21.40	22.85
CURF	9	22.18	0.77	0.26	3.47	21.00	23.40	21.41	22.95	21.60	22.76
PANF	12	21.80	0.44	0.13	2.03	21.15	22.60	21.36	22.24	21.52	22.08
SENF	12	22.30	0.69	0.20	3.12	21.30	23.60	21.61	22.99	21.86	22.74
STMF	6	22.17	0.15	0.06	0.69	22.00	22.40	22.01	22.32	22.01	22.33
SURF	6	21.93	0.68	0.28	3.11	20.65	22.45	21.24	22.61	21.21	22.64
ARAF	1	21.30	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
MANF	1	21.30	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
SCRF	1	20.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
COBF	3	21.88	0.00	0.00	0.00	21.30	22.55	0.00	0.00	0.00	0.00
HUAF	1	24.15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
KASF	1	21.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
MEXF	2	22.68	0.00	0.00	0.00	21.65	23.70	0.00	0.00	0.00	0.00
PAMF	1	20.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
SNIF	1	22.75	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
SONF	2	21.18	0.00	0.00	0.00	20.85	21.50	0.00	0.00	0.00	0.00
URAF	2	22.95	0.00	0.00	0.00	22.50	23.40	0.00	0.00	0.00	0.00

Table 4.92-Females Northern South America.Levels of Probability. Lenght of Lower Molar Series.

Sample	p	SNK	
Belem-San Nicolas Transect			
BELF/CALF		*	break
BELF/CURF		*	break
STMF/CALF		NS	
STMF/CURF		NS	
STMF/Manf	.001		break
Belem-Panama Transect			
BELF/CURF		*	break
BELF/CALF		*	break
BELF/Mexf	.8		
BELF/SENF		*	break
SENF/Mexf	.8		
SENF/SURF		NS	
SURF/Scrf	.8		
SURF/Argf	.7		
SURF/Kasf	.8		
SURF/Araf	.9		
SURF/PANF	.7		
Serra do Navio-Pamplona Transect			
SENF/Cobf	.9		
SENF/Pamf	.02		break
Panama-Cauca Transect			
PANF/Uraf	.05		break
CAUF/Sonf	.4		
CAUF/Uraf	.6		
Surinam-San Nicolas Transect			
SURF/Manf	.7		
SURF/Snif	.8		
Panama-San Nicolas Transect			
PANF/Uraf	.05		break

a significant difference with Manaus but no differences with Curralinho and Caldeirao.

b. Belem-Panama Transect - Belem is isolated. Curralinho, Caldeirao and Serra do Navio belong to the same set. Surinam is different from Serra do Navio but is not different from all localities farther west.

c. Serra do Navio-Pamplona Transect - There is a break between Serra do Navio and Pamplona.

d. Panama-Cauca Transect - Panama is isolated.

e. Surinam-San Nicolas Transect - No differences were found.

f. Panama-San Nicolas Transect - Panama is isolated. No further analysis was made.

g. Summary - The following set can be construed: Belem; Serra do Navio, Curralinho, Caldeirao and Santarem; Surinam and all other localities; excepting Panama.

4.10 INTERIM DISCUSSION: CORE AREAS AND INTERGRADATION

Maps figures 4.19 and 4.20 summarize the core areas of Black Eared Opossums in North and East South America. These areas were constructed after the analysis of each character and pairs of characters, along the transects had been put together as summaries. These summaries are necessary extrapolations of the statistical analyses. The nature of the material -both sexes are not always present in all samples, some samples are very far away from others, major and minor samples are not always located in

" strategic " points, made the interpretation subject to some guessing and the extrapolations in such cases do not constitute precise statements. However, this is a minor setback in the scale of this work.

The situation in the analysis of the Eastern samples is somewhat better than the Northern ones, since there are more samples, and the important area of the Serra do Mar is well represented.

The core areas are ensembles of characters varying together. In this area, the set of all characters shows less differentiation among the localities in the areas than with the adjaecent cores.

The situation of Eastern Brazil will be analysed separately from the situation of Northern South America.

4.10.1 Eastern Brazil

Four core areas can be determined for this region:

A. Sao Miguel to Espirito Santo

B. Floresta da Tijuca

C. Zona da Mata de Minas, Terezopolis and Sao Joao Marcos

D. Litoral de Sao Paulo to Santa Catarina

Area A has two localities very closely linked, Sao Miguel and Ilheus. There is no break between these samples with very low probabilities of significance for null hypothesis. Between Ilheus and Espirito Santo, there is differentiation, the similarity (percentual of non-significant differences) is only 56.5% and the probabilities are higher than the ones with Sao

Figure 4.19 - Core areas in Eastern Brazil.

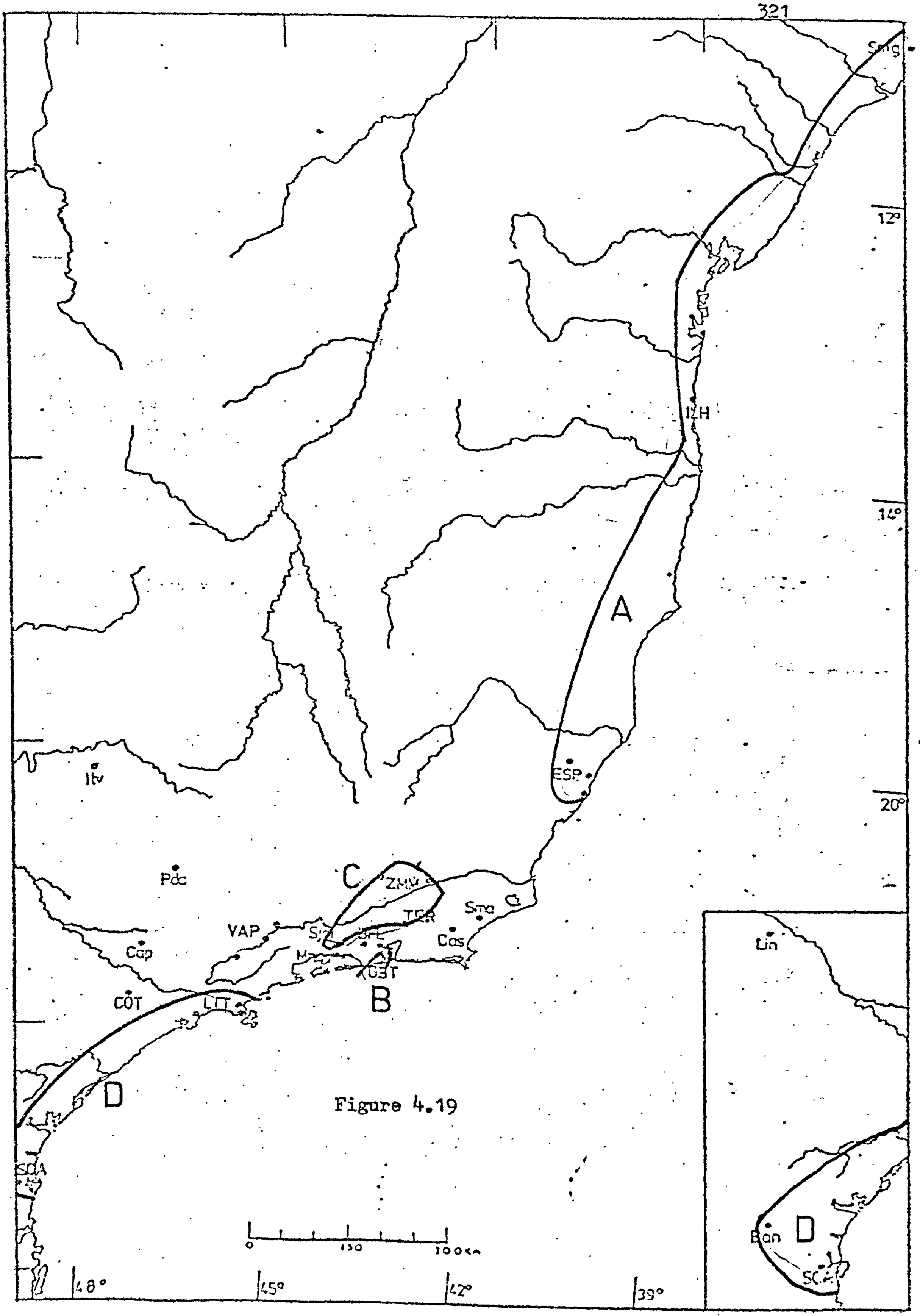

321
12°
14°
16°
20°
A
B
C
D
ESP
Pdc
VAP
Cap
COT
LIT
Cos
Lin
Ban
48°
45°
42°
39°
0
150
300km

Figure 4.19

Miguel.

Area B has a single locality, Floresta da Tijuca. All specimens were collected from a small area in that forest.

Core area C has an average similarity around 50%. Sao Joao Marcos is located in a tributary of the Paraiba river. The chief locality of Zona da Mata is in the bank of that river (Alem Paraiba). Terezopolis is a sample made near the city of this name, in the part of that region of the Serra do Mar which is a watershed between the tributaries of the Paraiba river and the stream which flows straight to the Atlantic. The probabilities of significance in average, are lower than those between Ilheus and Espirito Santo, for example, but are higher than the ones between Ilheus and Sao Miguel.

Area D has localities in the coastal plains and the Eastern slopes of the Serra do Mar. It is homogeneous, with about 55% similarity among the samples. The average probabilities of significant differences are low, lower than the average of the other core areas.

These areas intergrade one with the other through intermediate localities. Area A intergrades with B through the Serra de Macae and Casimiro de Abreu. In terms of similarity, Serra de Macae is a locality which belongs to both Espirito Santo and Guanabara. In terms of average probability the same can be said. For these two consideration, similarity and probabilities, Casimiro de Abreu is nearer to Floresta da Tijuca than to Espirito Santo.

Area B intergrades with area C through the Baixada Fluminense, which has the same levels of probability and similarity

with both Terezopolis and Floresta da Tijuca. Farther south, Mangaratiba is closer to area B than to the Litoral de Sao Paulo, in area D. The Baixada fluminense also intergrades area C and D, being however closer to Terezopolis than to the Litoral de Sao Paulo.

Area C has close links with area A through Espirito Santo, which is quite similar to Zona da Mata. There is no intermediate localities between the two areas. Espirito Santo is in some sense the intermediate zone between A and C.

Vale do Paraiba has a situation similar to Baixada Fluminense: it belongs at the same time to Cotia and Zona da Mata. However, Zona da Mata and Cotia are quite dissimilar.

Cotia and the Litoral de Sao Paulo seems to belong to quite different sets. However, Cotia and Bananal are very similar. Intergrading therefore occurs through the highlands west of Serra do Mar between areas C and D.

These core areas and intergrading zones between them will be discussed later. At this point, however, it must be emphasised that the degree of differentiation in the whole of the Coastal Atlantic Domain is not very high. The localities farther west (Campinas, Pocos de Caldas, Ituverava and Lins) do not show a pattern of differentiation in relation to the core areas and major samples which can be easily interpreted. For instance, Lins can both be set in the same ensembles of Santa Catarina and Zona da Mata. Further sampling is needed to clarify how the variation is in this large area. However, Lins is less similar than other localities with both the above-mentioned major samples. Is it a random result? Or is it a distance effect? Or, another possibility, is it indicative of the existence of other centres of differentiation?

4.10.2 Northern South America

The core areas of Northern South America were more difficult to construct. If the sampling was not so good for Eastern Brazil, in Amazonia up to now, almost no collection has been made in most of the region, with the exception of the mouth of the Amazon. Large areas have never been explored. The material I could assemble has no representation from the foothills and slopes of the east of the Andes. Therefore, the picture I can draw of variation of the Black Eared Opossum in that region must be considered provisional and subject to review in the light of future research. However, even this incomplete picture is interesting and rewarding in terms of the results I expected.

Four core areas may be drawn from the analyses of the transects when these are put together:

A. Serra do Navio

B. Surinam to Motopan

C. Panama to Cauca, Santa Marta and Rique

D. Belem to San Nicolas, along the Amazon

Area A has a single sample, with two close localities.

Area B comprises five localities. From Surinam to the west, the average probability of significant differences increases and, on the other hand, similarity decreases. Due to the distance and size of the samples, these results must be qualified: there is a differentiation along the transect and better samples may show that they are not the same ensemble.

The differentiation of area B to area C is not clear cut. Motopan and Truj Aragua differentiate strongly from Panama, less than Surinam does in relation to Kasmera, San Juan Nepomuceno

and Uraba. The area C is not very homogeneous, for instance, females of Cauca and Panama are very dissimilar, more dissimilar than Panama and the localities in the Pacific Coast.

The area D is non homogeneous. Belem is less similar to its neighbouring localities, Curralinho for instance, with 60% similarity, than Santarem is with the same samples --with Curralinho it has 100% similarity. The locality of Caldeirao may or may not be put in this ensemble, it is similar in the same way to Belem and Santarem but only slightly less similar to Serra do Navio. It shares a position similar to Chaves and Mexiana in the middle of the transect between Belem and Serra do Navio. The other localities in the Tapajos (Pau de Letra and Caxirituba) can be set in the same ensemble as Santarem. Going west, there is a progressive diminution of similarity and an increase in the average probability of differences. This phenomenon is less accentuated here than in the B area, but is more coherent, with an Nicolas having in fact the smaller percentual of similarity and the higher probability, while the picture in zone B is irregular.

The internal differentiation of the core areas in this region is larger than in Eastern Brazil. The first factor is undoubtedly the larger areas in northern South America. But the second is that the material does not give a clear picture and more possible core areas in relation to differentiation of characters can be possibly obtained with better samples.

The sample of Buenavista, farther away from any major one is more similar to Santarem than to Panama. No conclusion can be drawn from the results I have.

There are several areas of intergradation of individual

Figure 4.20 - Core areas in Northern South America .

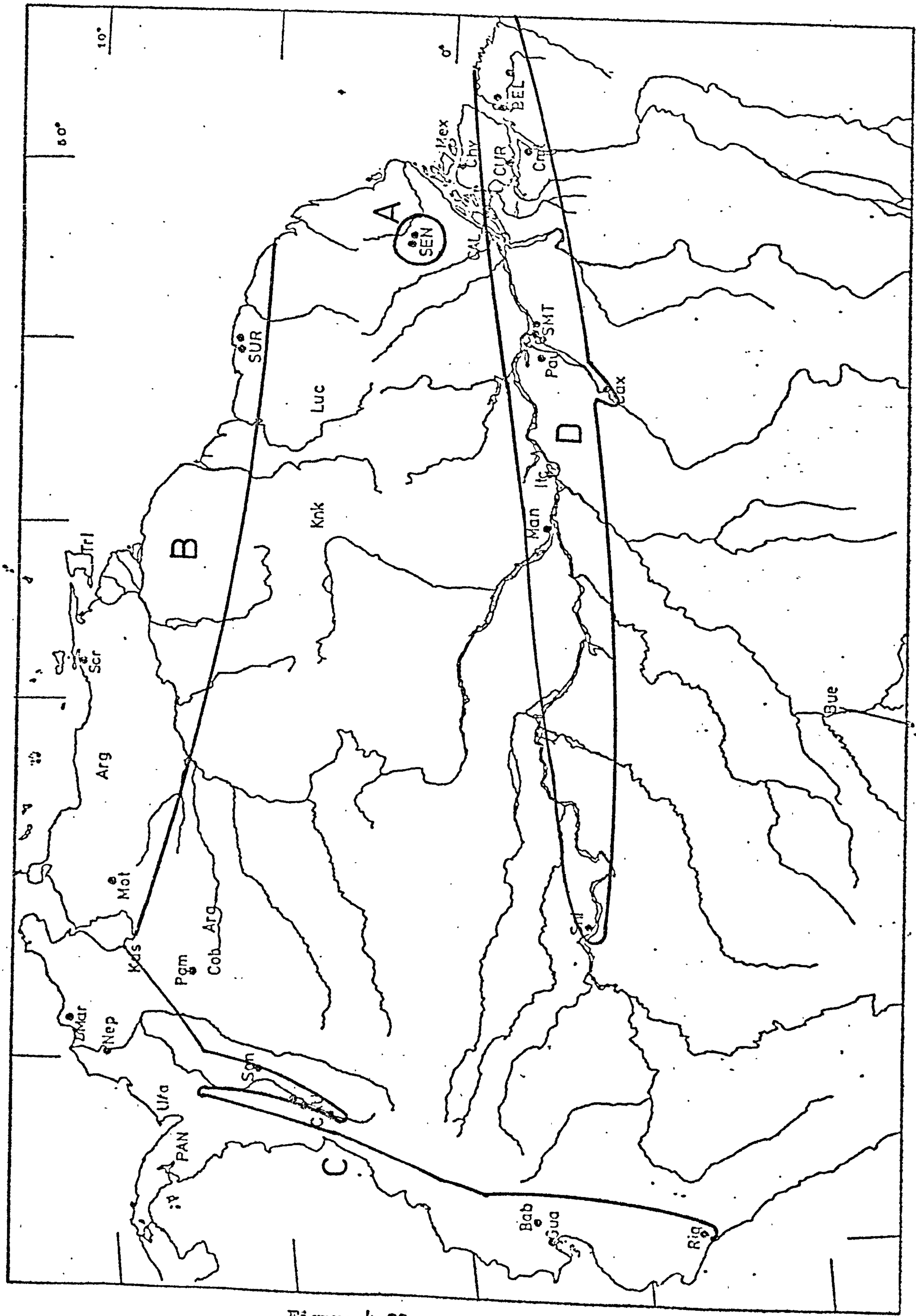

10°
0°
80°
A
B
C
D
SEN
Mex
Chy
CUR
Cmi
BEL
SUR
Luc
Knk
Pol
SMT
Cax
Man
Ilo
Tri
Scr
Arg
Mol
Kus
Pgm
Cob
Arg
Bue
Jil
Omar
Nep
Sam
Ura
PAN
Bab
Gua
Rio

Figure 4.20

characters as well as of the ensembles of them: Serra do Navio intergrades with Belem through Mexiana, Curralinho and Caldeirao. It intergrades as well with Santarem through the same samples. The Lucie river and Kanuku mountains can be set to belong to both Serra do Navio and Surinam. Arauca, Cobaria and Pamplona are difficult to set, showing similarity to both Serra do Navio and Panama. However, Serra do Navio which is almost three times more distant to Cobaria than Panama is at the same time more similar (percentual of 75%) and with lower probabilities of idfferences than Panama with the same sample (with 57% similarity). These results may suggest that factors other than distance were acting in the differentiation. Kanuku and Lucie River are intermediates between Surinam and Santarem, and these two localities display a good similarity. The intergrading between Zone area B and D exists through this region.

In the next chapter I shall try to extract some conclusions from the patterns these results of transect analysis have suggested.

CHAPTER V

CONCLUSIONS

5.1 INTRODUCTION

The distribution and geographical variation of mammals in South America is widely interpreted as being the result of dispersal of ancient taxa from a centre of origin in the Brazilian Highlands (e.g. Hershkovitz, 1969, 1972). On the other hand, the present distribution and variation of a number of lizards, birds, plants and insects has been explained in terms of episodes of geographical isolation due to the influence of climatic and consequent vegetational changes during the Quaternary. (Brown, 1975; Haffer, 1974; Spassky, 1971; Vanzolini & Williams, 1970). This is the Haffer-Vanzolini model, which postulates that during the Quaternary, the Neotropical region had alternate periods of dry and humid climates. During the dry periods the forests were restricted to small residual areas which acted as refuges for sylvatic organisms.

The present work examines the distribution and variation of Neogropical mammals in relation to the Haffer-Vanzolini model, with particular reference to the genus Didelphis. In chapter two of this paper, it is shown that when the broad processes described by the model are supplemented by studies of the particular ecology of individual taxa, the explanatory value of the model is amplified. The study of Didelphis shows that when the model is used in this way, the current distribution and variation of this genus can be explained in a more consistent and rational manner than by using hypothetical centers of origin. Less detailed studies on other taxa suggest that the model is of value for Neotropical mammals in general.

5.2 THE SPECIES OF DIDELPHIS IN SOUTH AMERICA

In Chapter three I have studied and discussed the spatial distribution of Didelphis in South America. Two groups can be easily distinguished on skin colouration, particularly on the colour of the ears. It is clear from the ecological studies that these two groups do no share the same geographical and ecological pattern. Moreover, there are also ecological variations within each group. The first group to be discussed is the "White eared opposum". Up to now, this group has been considered a single species: Didelphis albiventris (c.f. Chapter one). However, the evidence here analysed does not support this commonly-held opinion.

Some populations are isolated in the Roraima Mountains. There are no intermediate populations between this group and other populations of "D. albiventris." The status of these populations can not be assessed here, as there are not enough data about the environment where they live and did not have access to specimens from Roraima. However, it is known (Hershkovitz, 1969) that they live at high altitudes in these mountains. O.A. Reig (personal communications) informed me that in the Gran Sabana Domain, no white eared opossum was ever collected, nor do they exist in the Llanos del Orinoco. It seems that the Roraima population live in conditions which are similar to the habitat of the white eared opossums of the Andes, which usually live about 2000 meters, in the Oreal domains (see fig. 3.6). In chapter three, it is shown that these two groups live in ecological conditions quite different to those exploited by other populations. They are separated by several vegetational formations but principally by the forests which occur east of the

Andes. The only apparent link is between the populations of the Monte desert and the ones in the morphoclimatic domain of the Puna (Chapter three). Therefore, the "species" Didelphis albiventris may well turn out to be a Formenkreise, comprising at least two semi-species. The status of the Ayuantepui populations in Roraima can not be discussed here, but they could be a third form, a full species or a semispecies closely related to the group. I am studying the variation in this group and preliminary results seem to support the above assumption. More research is needed to clarify this issue. For the moment, two sub-specific epithets may be used.

The Black Eared Opossums are restricted to Rainforests and cloud forests (Chapter three). There is no evidence whatsoever for the existence of these Opossums in either the Caatingas or the Cerrados. The populations of Eastern Brazil are separated from the ones in the Roainforests of Northern South America. The Northernmost record in Eastern Brazil, at Sao Miguel, State of Alagoas, is about 1400 kilometers south of the southernmost locality on the coast of Northern South America, at Anil, State of Maranhao. It is clear that these two ensembles of populations are geographically isolated.

The study of correlations between pairs of characters (chapter four) demonstrated that the northern populations have different correlation pleiades from those of the Eastern Brazil ensemble.

One conclusion which can be drawn from the differences in correlation pleiades, together with the fact of geographical isolation, is that these two ensembles of populations constitute two different biological species:

Didelphis aurita Wied

Didelphys marsupialis Wied, Beitr.Naturg.Brasil., 2, 1826:387 (not Linnaeus, 1758)

Didelphys aurita Wied, loc. Cit.,1826:393

Didelphys azarae Wagner, Schrebers Saug. Supp., 3, 1843: 38 (part; not Temminck, Monogr. Mammal. 1,1825:30; not Tschudi, Faun.Peru.1844:143)

Didelphys cancrivora Burmeister, Syst. Ubers. Thiere Brasil.,1,1854: 129 (Not Gmelin Syst. Nat. 1,1788: 108)

Didelphis marsupialis, var. typica Thomas, Catal. Marsup. Brit. Mus. 1888: 323 (part)

Didelphis marsupialis aurita Cope, Am. Nat. 1889: 129

Didelphys koseritzi Ihering, Mamm. Rio Grande do Sul, 1892: 99

Didelphis marsupialis cancrivora Bertoni, Faun. Paraguaya, 1914: 68

[Didelphis] leucoprymnus Matschie, Sitz.-ber. Gesell naturg. Freunde 8, 1916: 268 (in list of species)

Lectotype: American Museum of Natural History number 836, adult male, mounted skin and skull (selected as lectotype by Avila Pires, 1965)

Type locality: Vila Vicosa, Rio Peruipe, State of Bahia, Brazil.

Distribution : Eastern Brazil in the Tropical Atlantic and Araucaria Domains, extending to neighbouring parts of these domains in Paraguay and Argentina.

Obs.: The Black eared opossum of Eastern Brazil.

Didelphis marsupialis Linnaeus

Didelphis marsupialis Linnaeus, Syst. Nat. 1758: 54 (part)

Didelphis karkinophaga Zimmermann, Geogr. Gesch. Thiere, 2, 1780:266

Didelphis cancrivora Gmelin, Linn. Syst. Nat. 1, 1788: 108

Didelphis marsupialis var. typica Thomas, Catal. Marsup. Brit. Mus. 1888: 323 (part)

Didelphis aurita J.A. Allen, Bull.Am.Mus.Nat.Hist. 9, 1897: 43 (not Wied, 1826)

Didelphis richmondi J.A. Allen, Bull.Am.Mus.Nat.Hist., 14, 1901: 175

Did[elphis] austro-americana J.A. Allen Bull. Amer. Mus. Nat. Hist., 16, 1902: 251 (ex Oken, 1816)

Did.mes-americana J.A. Allen, Bull. Amer.Mus.Nat.Hist. 16,1902: 251 (ex Oken, 1816)

Didelphis marsupialis marsupialis J.A. Allen, Bull.Amer.Mus.Nat.Hist., 35, 1916: 502

Holotype: Philander, maximus, orientalis Seba, Thesaurus, 1, 1734: 64, pl. 39, by primary designation, Linnaeus, 1758. (Gardner, 1973).
Type locality: Guianas, restricted to Surinam by Thomas (Proc. Zool. Soc. London 1911:143).
Distribution: In Central America "From central Tamaulipas in eastern Mexico at elevations generally under 4500 feet, through eastern San Luis Potosi, Veracruz, eastern Puebla and Oaxaca to the Isthmus of Tehuantepec , thence southward from coast to coast through Mexico and Central America to northern and western Colombia, western Ecuador, and northwestern Peru" (Gardner, 1973). In northern South America, in all domains between Amazonia and the Caribbean Sea, excluding the Ayuan-tepui, and the Paramos. Extending south through some fringe forests in the Brazilian highlands and in the cloud and rainforests in the slopes of the Andes up to Bolivia.
Remarks: The characters studied of both forms are in Chapter four. In chapter three the distribution of these two taxa is studied in detail. See opendix four as well for a discriminant analysis and for the means and standard deviations of these two forms.

5.3 VARIATION IN BLACK EARED POSSUMS

The first study I must discuss concerns the differences in correlation pleiades. There are four sets of correlation pleiades:Two for females and two for males. Males differ in shape from females in both the Eastern Brazil and Northern South America ensemble of populations. More research must be done in order to understand these pleiades. One hypothesis for the differences between sexes is that the growth of females slows down because they usually get pregnant before growth stops (Chapter 3 and Cerqueira). The differences in growth patterns could also be due to different canalization processes in ontogeny. My data and the level of analysis used here cannot allow me to decided what factor (or factors) are responsible for the phenom-enon and more research is needed to clarify the point. Van Valen (1965) pointed out that morphological variation enlarges the niche width, and if females and males of the same species have some morphol-ogical differences, this may be advantageous in exploiting the

resource space. There is some controversy about the validity of this hypothesis (Soule & Stewart, 1970; Straney, 1978).

The basic assumption of the Haffer-Vanzolini model is that differentiation among populations in South America was accelerated by climatic change. In Chapter two these related climatic/vegetational changes were discussed. A reasonable working hypothesis is that the Atlantic Forest was linked in the past with the Hylea. The habitus of the two species of the Black Eared Opossums is quite similar (and up to now, all these opossums have been considered a single species). Assuming the geographic speciation (or allopatric) model, these two species were linked in the past as a single panmitic population. The last glacial maximum was the time when the Atlantic Forest and the Hylea separated (not discussing former disjunction during previous climatic changes). The pluvial maximum which seems to have preceded the glacial maximum, has been the time of the link between the two rainforests. The breaking of this link would thus have occured before 21,000ybp (Ab'Saber, 1977b), beginning the process of separation of the two ensembles. If the above hypotheses are correct, the basic assumption of the Haffer-Vanzolini model holds as an explanation for the speciation of the Black Eared Opossums in South America.

The intra-specific variation within each ensemble was studied in chapter four. In this case, the model in question had more specific previsions: refugia of rainforest existed and forest animals were restricted to that refugia during arid periods. As I discussed in chapter two, the concept of refugia must be qualified area of the refuge, geographical situation, differences in vegetational conditions, ecotones with surrounding areas and possible links among the refuges create a situation in which an area could

5.4 CONCLUDING REMARKS

I have asserted that climatic change and fluctuation must be taken into account for the zoology of mammals in South America to be understood. Geological and other evidence indicates that climatic variations changed the spatial distribution of morpho-climatic domains of vegation. The study of the geographical ecology and variation of the genus Didelphis gave results which are in general in good accordance with the initial hypothesis proposed in chapter one and with a qualified acceptance of the Haffer-Vanzolini model (and consequent hypotheses)discussed in chapter two.

More work is indeed necessary to detail not only the paleoloandscapes but also the Zoology of mammals in South America. The refuge theory appears to provide a suitable framework for such research. Punctuated equilibria, the vicariance model and the Red Queen hypothesis may be integrated in the future, in a single theoretical body. The full implications of these theories were not discussed in depth here, but, I hope, more theoretically-minded colleagues may take note of my attempt outlined in Chapter two and use the Refuge Theory as a point of reference in such efforts.

APPENDIX I

THE MORPHOCLIMATIC DOMAINS OF SOUTH AMERICA

THE MORPHOCLIMATIC DOMAINS OF SOUTH AMERICA

1. Amazonia

The Humboldt's Hylae (Equatorial Amazonian Domain) - In a large area North and South of the Equator lies the largest rainforest of the world. The region has a super humid equatorial climate. This climate is not uniform throughout the region, as is to be expected in such a large area and there is variation inrainfall, temperature, and humidity throughout the year. In some areas, the pluviosity is much higher than in others, some regions with no dry season and others with at least one month of drought (Nimer, 1977). Enclaves of several types occur inside the Hylae: Cerrados (Veloso, 1966), Grasslands and Parklike formations (Japiassu, 1974; Vanzolini, 1972), man-made clearings (Vanzolini, op. cit.), the Caatinga of Rio Negro (Hueck, 1972; Takeuchi, 1960c), etc.

The general features of the forests are: an evergreen forest, dense and tall (Veloso, 1966), very rich in species (Hueck, 1972, Vanzolini, 1952), well-stratified and with emerging trees which overtops the forest ceiling. The forest extends from the Atlantic towards the Andes without interruption (Fig). Surrounding the corridor of the typical Amazon forest there is both to the north and south, a semideciduous forest. This forest is the transitional belt between the Amazon and the other domains (Kuhlmann, 1977; Ab'Saber, 1966).

The forest in the core area has three different facies (fig which are caused by the geography. The first is the Mata de Terra Firme, which is located in the high ground and is never flooded. This Mata is the most important in terms of area. The second type is the Mata de Varzea found on seasonally flooded riversides and on back

swamps. And finally, the Igapo, permanently flooded forest which has little area expression (Vanzolini, 1972). There is differences in the composition and structure of these kinds of vegetation. The fauna must show differences also, but there are no ecological studies about the succesion of faunas from the river to the high plains. However, some mammals appear to occur chiefly near the rivers (Cerqueira, 1976, Hershkovitz, 1977).

Ducke & Black (1953) in their review of the Amazonian Phytogeography, noticed differences in composition among several areas of the Hyalaea. Hueck (1972) considered fourteen different forests while Muller (1973) showed four different Vertebrates "dispersal centers" in this region. The state of knowledge makes it difficult to divide the valley with precision, and since transitional areas occur sometimes, it is not worth trying such a division here. Nevertheless, these recognized different regions inside the domain are important to the understanding of the past of the forest, chiefly when they are considered together with the enclaves, the "inselbergs" (Hurault, 1974; Granville & Sastre, 1974), etc.

The Roraimo-Guainan Domain is like a gigantic enclave surrounded by Amazonia . . . Certain other facies occur in the coastal periphery of the domain but are neither enclaves nor variants but facies which appear on ground gained over the sea. They are the "Savanas" of Coastal Guianas, the Campos of Marjo and the Mangroves. The latter is a vegetation which is one of the oldest known therefore being older than at least the majority of the vegetation discussed here.

2. The Pacific Rainforest (Pacific Equatorial Domain).

From the Panamanian isthmust to Ecuador through the Andean foothills and the plains of the Pacific littoral of this region, lies a large Pluvial forest area. The rainfall is among the highest in the world (Haffer, 1970). The Caribbean rainforest is linked with this forest but some authors doubt the identity of the two biomes (Hueck, 1972). There is a large number of forms (Cuatrecasas, 1958), but the region is not well-studied, although two facies are recognized, the Plains Rainforest and the Mountains Rainforest. Grass and palm swamps and lagoons cover large areas in the lower Rio Atrato Valley (Haffer, 1970). In the plains, swampy rainforests are common but toward the south, deciduous species appear with the decrease of moisture

The fauna of the region has elements of Northern origin, but as a whole, the region is balanced towards the Neotropics (Cabrera & Willink, 1973; Hershkovitz, 1972; Savage, 1966).

3. The Atlantic Forest (Tropical Atlantic Domain: The Sea of Hills).

This domain extends from the parallel 7°S to near the parallel 30°s. In the Northern parts it is a narrow strip but in the South it is broader, chiefly near the Tropic of Capricorn. With such a large variation in latitude the temperature varies also but the humidity an rainfall are high in the whole area. The high rainfall operating through the Quaternary has created the characteristic shape of its hills with their typical half-orange top. These facies are caused chiefly by the chemical weathering under the forest cover (Ab'Saber, 1966b; B.garella & Andrade, 1965; Bigarella et.al., 1965). There are variations in the composition and structure of the forests from North to South. This variation is not only clinal but also caused by historical reasons,

the clines related to differences in rainfall, topography, etc. North of the city of Salvador, in the State of Bahia, and as far as the mouth of the Rio Sao Francisco, the area is less humid and perhaps, with a Tropical Deciduous Forest. Southern Bahia Forest - the Hylaea Baiana- has some similarities with the Amazonia (Veloso, 1966).

The coastal forest of this domain must be distinguished from its counterpart in the mainland. The Coastal forest is the Evergreen Atlantic Forest. In the NE of Brazil, it receives the influenceof the air masses which came from the lower latitudes of the Atlantic while the forest which covers the slopes of the Serra do Mar and Serra da Mantiquiera is under the influence of South Polar masses. The vegetation in the mainland which reaches the coast between the Rio Paraiba and the Ric Doce is less humid and partially deciduous. As a whole the region has two well-defined seasons: a dry season and a rainy one. The forests are tall and dense but without emerging trees, the number of lifeforms is lower than in Amazonia but still large. In the forested slopes there is a large amount of Lianas, vines and epiphytic plants. The greater the moisture the denser the forest. Cerrados occur as enclaves inside the domain, in the Central South Uplands Evergreen Forest (Ab'Saber, 1970; Veloso, 1966).

In higher altitudes there are Araucaria woods, isolated Araucaria trees and altitudinal meadows. The existence of mountains intercepting the air masses creates several types of vegetation. An ideal transect through the Serra do Mar and Serra da Mantiquiera is shown in Fig. . The topography in this domain, together with the one in the Araucaria Highlands Domain, makes this region one of the most interesting areas in South America in biological terms and also in terms of scenic values of the landscape.

The ecology of the region, the structure of the forests, etc., is not well-known but littl work on the subject has been done (Aragao 1961; Coutinho, 1962; Davis, 1945; Lima, 1960; 1966). In one important work Aragao (1961) discussed the similarities between some isolated forests of Northeastern Brazil and the forests in the State of Rio de Janeiro. He noticed that rainfall and temperature can not explain these similarities and that the two forests are cloud forests. Forests with this facies show an intense growth of epihytic plants and Bromeliads in the Southern slopes but although other forests in the same region have the same rainfall and temperature, they do not have the same features. He concluded that the phenomenon is caused by differences in insulation and atmospheric moisture. These differences are related by the ascent of air masses loaded with moisture in the slopes which causes the condensation of fog and lengthy rainfall. The position of the slope in relation to the path of the sun, with differences in insulation is another factor to be considered. The importance of Aragao' article is its emphasis in the role of local topographic and mesoclimatic conditions. As will be discussed later, these topographical features have been of paramount importance through the Quaternary.

4. The Cerrados (Domain of Cerrados)

There is an extensive area of Savanas in South America. These savanas have their core areas in the Highlands of Central Brasil. Savana formations also occur scattered through Amazonia, Tropical Atlantic and the Caatinga Domains. Approximately 1.8 million of km^2 of Brazil is covered by Cerrados.

The extensive highlands of the domains have altitudes varying from 350 to 600m, the surface being slightly undulated but without large elevations with the exception of some in Goias and Mato Grosso

The climate has two seasons, one rainy, the other dry. Cerrados are not exerophytic. It was demonstrated that the vegetation is dependent on a humid or sub-humid condition (Reis, 1971; Ferri, 1955; Ferri & Coutinho, 1958; Veloso, 1966). The climatic condition which causes the appearnace of Cerrados is the same as that which causes the appearance of forests (Reis, 1971). However, Cerrados occur outside the core area, such as in the intermediary belt with the Caatinga in North-Eastern Brazil, where a drier condition does not restrict the Cerrados which is a component of the vegetational mosaic.

Several types of soils exist in the Cerrados but the most widespread are the oligotrophism in the soils and this kind of vegetation (Arens, 1958; 1963). The Cerrados do not have deficiency of water and their xerophytic facies is due to the oligotrophism (Arens op.cit.; Ferris, 1962). Not all savanas in Latin America have these characteristics,some existing due to reistraned drainage (Beard, 1953; Goodland, 1971). Aluminium is abundant in Cerrados soils and Goodland op.cit.) suggested that these old soils with large contents of this metal are very important to the vegetation, which has adapted to it. Xeromorphic appearance may also be related with them.

The domain shows a varied landscape, with several kinds of Cerrados ranging from almost pure grasslands through characteristic parkland to the Cerradao's wooded savanas. Along the rivers there are gallery forests. These fringe woods have a composition and structure which is linked with the surrounding domains. Extensive grassland enclaves, as well as tropical seasonal rainforest and tropical deciduous forest occur in the area too. Sometimes these enclaves are very large such as the Mato Grosso de Goias, South of the State of Goias (Rainforest) and the Campos de Vacaria, South of the State of Mato Grosso (Grasslands) Veloso, 1966).

The Cerrados interdigitate with the surrounding domains existing within them and also in the intermediate belts, where a complex mosaic appears. The occurrence of Cerrado in te belts has been linked with a local distribution of soils (Askews et al. 1971; Cerquira, 1976; Vanzolini, 1976).

The large Pantanal de Mato Grosso, a flooded plain west of the State of Mato Grosso is a complex of sanvans, gallery forest and overflow prairies. It has poor soils and restrained drainage and forms an intermediate belt between Cerrados and the Chaco.

The fauna of the Cerrados is not characteristic (Vanzolini, 1963), having few proper forms, the majority probably at sub-specific level. They share elements with the Chaco, the Caatinga and the surrounding forests.

5. The Gra-Sabana (Roraimo-Guianean Domain)

In the high altitudes of the Guiana Shield, extending along the lower mountains of Southern Guianas, a large area of Savana vegetation is found. The area is not well-known, poorly inhabited and studied only by few expeditions. Nevertheless, it is known that there is a large endemism of plants (Tate, 1939) and birds (Mayr & Phelps, 1967), but only two mammals are different from those in the surrounding region (Hershkovitz, 1969, 1972; Tate, 1939).

There are several high mountains with more than 2000m altitude, including the Pico da Neblina, the tallest mountain in Brazil. Generally-speaking, the topography is one of Plateaus with quasi-vertical slopes, and savana vegetation. In the slopes and ravines there are dense forests (Cabrera & Willink, 1973; Vila et al., 1965).

Its floristic affinities are with the Cerrados and the Southern Brazilian Mountains (Cabrera & Willink, op.cit.; Tate, 1939). The Avian fauna, with 29 endemic species out of a regional total of 96, has affinities with the fauna found in the Andes, North Venezuelan Mountains and Brazilian Highlands (Mayr & Phelps, 1967).

Information on climate and soils is scarce. In the Rupununi Savana of southern Guiana, restricted drainage seems to play the major role in the formation of the Savana vegetation (Beard, 1953). There is also altitudinal zonation in the higher parts of the region.

6. The Domain of the Llanos del Orinoco

North of the Rio Orinoco there is a large, gently ondulated lowland area, covered by grasslands. These grasslands are interrupted sometimes by savana-like vegetation. Deciduous gallery forests can also be found. There is a high pluviosity in the rainy season, followed by a very dry season (Cabrera & Willink, 1973; Hueck, 1972) caused by the monsoonal circulation of the air masses. Without stepped topographic features there are no conditions for the maintenance of rainforests. Fire, perhaps combined with restricted drainage, plays a major role in the existence of these facies. Some authors believe that man caused the fire (e.g. Hueck, 1972) and consequently the facies of the landscape. But even if it is true for today, the existence of plants adapted to that environment suggests that the major role is played by ecological factors.

The fauna of the Llanos is not exclusive to the area, but rather, is shared with the neighbouring regions (Cabrera & Willink op.cit.; Hershkovitz, 1969, 1972).

7. The Equatorial Andes Domain

The nuclear area of this domain extends in a narrow strip from Central Bolivia to Southern Colombia in the foothills of the Andes. A complex altitudinal zonation, as well as differences due to latitude exists.

The region has high rainfall and the topography causes the emergence of cloudy forests (cf. discussion in the section referring to Tropical Atlantic Forest. cf. also Aragao, 1961). There is little information on its soils and climate. The rainfall in the mountain and in the eastern slopes, reaches 2000mmto 4000mm annual rainfall. There is two rainy and two dryer periods but no true dry period (Hueck, 1972). The altitudes vary between 500m to 3500m (Cabrera & Willink, 1973).

There are several forest subdivisions in the region. In Bolivia two kinds of Yungas Woods at low and middle altitude and the Cejas Woods in higher elevations (Hueck, 1972), while in other parts the distribution of vegetation issimilar but with different composition (Cuatrecasas, 1958). The topographical complexity has a corresponding complexity in the vegetation and faunation, with several forms, at least at subspecific level, occuring throughout the region (Cabrera, 1961; Cabrera & Willink, 1973; Cuatrecasas, 1958; Hershkovitz, 1968, 1972)

8. The Domain of the Caatingas (Semiarid depressions between uplands).

A semiarid, tropical and subequatorialregion, with azonal position (Ab'Saber, 1971), likes in Northeastern Brazil. The Domain occupies 700,000 to 800,000 km^2 of Brazil.

Although at present, there is low weathering, the erosive

process shows large pediplanation. Bare rocks and Inselbergs are frequent. The rhythm of rainfall is highly irregular averaging from 350mm to 600mm each year. The nature of the rainfall causes intermittent and extensive drainage systems to appear. The barrenness of the domain facies is caused more by the irregularity than by the presence of rain. Some years, the rain is so scarce that the drought reaches catastrophic proportions.

There is a large variation in the amount of rainfall everywhere in the domain. Throughout the year, average temperatures are also high and whenever the monsoonal winds do not bring the moisture, the drought comes.

There is no high altitudes in the region, although there are some highlands and plateaus (Chapadas, in local vernacular). However, even these are enough to intercept the moisture of the air someitmes removing it and not allowing its passage to the mainland.

The landscape is monotonous, large flatlands with the Chapadas in the background cut off by the ravines. During the dry season these barren lands are very desolate, with scattered leafless trees and bare grounds varying from quasi white to red. The dust covers the traveller who finds the sands and sharp edged stones from the dry river beds along his way. When the rain comes, there is a sudden change. It would be difficult to find his same path again. In the drought, the landscape changes to a dull grey and only the Juazeiro (Zizyphus joazeiro), the cacti, the palm-trees and some other plants retain their green and leaves. But with water, the greyish colour also changes to several tonalities of green. Flowers bud open everywhere, the soil is no longer visible, and the river beds are hidden by the sometimes torrential waters. Thousands of butterflies and other insects are prey for birds which feed the hawks.

The experience of two seasons in the Sertao is unforgetable.

The most widespread kind of Caatinga is the thornbush. Some areas may have tall thorny succulent trees grouped in woodlands. Parklands are also common. There is no study yet of the influence of soil, topography and local mesoclimates found in the distribution of the different kinds of Caatingas. The RADAM project has surveyed some areas in the north of the region showing the mosaic of several types of Caatinga but no survey has been made (or published as yet) on the rest of the region (See BRASIL in the bibliography). These charts are very good for the intermediatte belt between the Cerrados and the Caatingas and a study of its lizard fauna recently has been made (Vanzolini, 1976). This study confirms an earlier hypothesis that Caatinga does not have a proper lizard fauna but only "a subset of the general fauna of the great cis-Andean diagonal of open formations." The same may be said about birds (Cabrera & Willink, 1973). The mammals are not abundant in the Caatingas but the Mocos (Kerodon rupestris) inhabit the bare stones groups and several others, like Didelphis alibventris (the white eared opossum), may also be found in the proper Caatinga. The mammals, however, are not absent in the region, particularly, along the rivers in the gallery forests and the Brejos. The Brejos are regions where the free ground water reaches the surface or is near it, or where local orography allows condens-ationof atmospheric moisture with consequent local high humidity (Aragao, 1961). Rodents, so conspicuous everywhere in South America, are absent in the typical Caatinga (Baltazard, 1968; Cerqueira, 1976) but are common in the Brejos and in some woodland Caatingas.

9. The Caribe-Guajira Domain

In Northwestern Venezuela and Northeastern Colombia lies

an arid area under the influence of Caribbean monsoons. The rainfall averages between 400 to 600mm/year, with high temperatures, 28° to 29°C at sea level, 24°C in the Highlands (Hueck, 1972). The Aliseos winds blow continuously but do not carry moisture, and although the rainfall varies from year to year, sometimes there is no rain at all. The consequences of the climate can be seen in the soil which is rocky, neutral or basic, sometimes salted. There is no humus and the soil remins dry for long periods of the year. Erosion is intense. The rainfall increases wherever the winds meet the mountains (Cuatrecasas, 1958).

The vegetation is characteristically xerophitic, with cactuses and thornbushes with coriaceous leaves. Some area actually has no vegetation due to the existence of salt, concentrated in the bottom of dry lakes and lagoons. There is some similarities between the Guajira, and the Chaco and Caatinga, but the species, nevertheless, are quit different. A humid forest may develop with the help of altitudes. (Cuatrecasas, 1958; Hueck, 1972).

The belt which surrounds the domain is more wet under the influence of the Andes.

There is no apparent faunal differentiation in the region since the species that occur there are of large distribution (Cabrera, & Willink, 1973). However, the cottontail rabbit Silvilagus floridanus is characteristic of the region and can also be found in some other dry lands of Northern South America (Hershkovitz, 1950). S. Floridanus is the viccarian of S. brasiliensis in the domain. The latter is excluded from this region and a few others by the former.

10. The Chaco (Central Chaco Domain)

The Chaco lies in the middle of South America occupying a

large area which covers almost the whole of Paraguay, Southern Bolivia Northern Argentina and a small area in Brazil. In Ab'Saber's concept, (1977) the nuclear area of the domain corresponds primarily to the Boreal and Central Chaco and the Gran Chaco. The more humid Eastern Chaco, is considered by him to be an transitional area.

The chaco is constituted by plains with low altitudes (less than 200m). The altitudes are never higher than 350m (Hueck, 1972). These plains are continuous towards the south with the low grounds of the Parana Valley but are surrounded by highlands and mountains in the other cardinal points (Fig.)

In the area, before the rising of the Andes, marine transgressions occured and clay limestones, salt and gypsum were deposited. In the Cenozoic the area has been receiving continental deposits and the superior layers are clay and sandy loess and the lower ones are marls (Harrington, 1962, Hueck, 1972; Mendes & Petri, 1971). The soil is brown and without humus, due to the climatic conditions being very alcaline. There is little moistrue in the soils and the free ground water is found very deep. Dunes and salted soils are not an uncommon feature..

The Chaco is a region of low atmospheric pressure in the middle latitudes of South America. The Central Chaco area is the one with less pluviosity in the whole Chaco. This is the core area for features on the Chaco, since under the climatic influence the arid facies of the soil and vegetation are accentuated. The temperature is high, decreasing from North to South.

The vegetation is a deciduous xerophitic woodland (Cabrera & Willink, 1973). There is a low density of trees which allows the insulation of the ground and the consequent development of herbs, with grasses, cactuses and Bromeliads. The typical woodlands are the

Bosques de Quebrachos (Genera Aspidosperma and chiefly Schinopsis). The Quebrachos can also be found in the transition belts of Eastern Chaco (Ragonese & Catiglioni, 1970). When the soil is drier and with higher content of salt, a Bosque de Algârrobo (Genus Prosopis) may develop. There are other variations, such as halophytic vegetation in high salted ground, Palm Savanas in low deep free ground water a areas, gallery forests near streams and swamps, etc.

The Fauna is characteristic but it is the local variant of the large belt of open formations which ranges from the Caatinga through Cerrados to the Chaco (Vanzolini, 1976). It may be hypothesised that sister groups are to be found in Chaco and Caatinga, the few faunal lists extants (Wetzel & Lovett, 1974; Moojen, 1943) pointing to that. However, some animals are exclusive to the Chaco, such as the "extinct" alive Peccary Catagonus (Wetzel et al., 1975) the Cricetids Graomys pearsoni (Myers, 1977), and Pseudoryzomys wavrini (Hershkovitz, 1962) all of which do not have their equivalent in the Caatinga. However, Holochilus of the Chaco is quite similar to Holochilus of Northeastern Brazil (Cerqueira, 1976).

11. The Pacific Coastal Desert Domain

Between 5° and 30° latitudes, in the Pacific coastal strip of South America there is a desert area with warm and dry climate. The rainfall in some parts is almost absent, with some years having no rain at all. In some parts the ground is very salted. Only along the river banks and in higher altitudes can some permanent veget ation exist. The rivers are formed by the rains and by the thawing of Glaciers in the Andes.

Sometimes, an arborescent vegetation, the Lomas, can be found along the mountain foothills and near the sea. The existence

of this vegetation is made possible by the condensation of fog.

There are some similarities between the Flora of that region and the ones of the Chaco and the Caatinga. However, the majority of forms shows more relations with the ones in the Andes and Patagonia (Cabrera & Willink, 1973; Hueck, 1972; Weberbauer, 1945).

12. The Puna Stepes and Bolsones in the High Andes (Puna Domain).

The Puna is formed by high plains which lie between the parallels 15° to 27° south. Typical of the Puna are the large pockets of rather flat areas, surrounded by mountains. It has a characteristic vegetation and Fauna. The boundaries of the domain presently coincide with the distribution of the Vicuna (Vicugna vicugna) a Camelid (Hershkovitz, 1972).

The region has an average altitude ranging from 3200 to 4400 meters (Cabrera & Willink, 1973). The typical vegetation is grasslands in the rocky slopes of the terrain ondulations (common genera being Festuca, Poa, Bromas, etc.) Some large areas are very arid, and there are even salted deserts (e.g. Salar de Uyni, Departamento de Potosi, in Bolivia)

The rainfall is not high in the Puna, ranging from 500mm/yr to 700mm/yr. The pluviosity varies from higher in the north to lesser in the south and west. This variation is linked to the topography's influence on the circulation of the atmosphere (Cabrera & Willink, 1973). The temperature ranges from -18°C to +16°C (Hershkovitz, 1972). Under these severe conditions, a steppe developed with its own pastoral fauna. The grass steppes cover large areas, the grass occuring in tufts and surrounded by bare ground. In flat areas, where the drainage is obstructed, marsh peats develop in the banks of the bogs, frequently occupying them entirely. The pit-bogs are formed

chiefly by Distichia, a Juncaceae, but not by Sphagnum, which occur only in small amounts (Weberbauer, 1945).

In the South the climate is more arid and the vegetation has links with the Monte. In the more humid North, there is a shrub steppe with several plants collectively named Tola (Genera Parastrephia, Baccharis, Senecio, etc.).

In rocky terrains from 3700m to 4500m altitude, sometimes reaching the snow line, one can find polylepis woods. Where the area is more arid, there is only the grass steppe, shrubs being restrained at depressions or high level free ground water areas.

Several genera of plants (Parastrephia, Lampaya, etc.) and mammals (Vicugna, Punomys, etc.) are endemic to the Domain (Cabrera & Willink, 1973; Hershkovitz, 1962, 1972).

13. The Araucaria Highlands Domains

In the highlands of Southern Brazil, with average altitudes ranging between 850m to 1300m, lies the core area of a mixed rain forest, dominated by the Parana Pine, Araucaria angustifolia.

The climate of the area is subtropical, and neither the winter nor the summer is vigorous. The rainfall is high, with no less than 1000mm/year (Andrade, 1968) and although the soils are varied latossols are nevertheless very frequent (Queiroz Neto, 1968).

The characteristic vegetation is a mixed Araucaria -broadleaf rainforest. The Araucaria gives the phytophysiognomic facies of the vegetation (fig.). However these forests are complex formations with large numbers of species, the larges number being the Lauraceae. It is interesting to note that several genera of plants which occur in this formation occur too in the Andes, which acts as a dispersal area, as for example, Gunnera, Podocarpus,

Berberis, etc. (Klein, 1975, and references in this paper). The inferior altitudinal limit of the Araucaria is 500m. Where the river valleys are, sometimes very deep, (Maack, 1965), the altitude falls in less than this height; In the west, substitution of this formation by a boradleaf forest will thus occur. In the east, a mixed raiforest the slope of the Serra do Mar occurs (Hueck, 1972; Klein, 1975; Maack, 1965; Veloso, 1966). The former is a formation charact eristic of the Parana-Uruguai river basins which make up the Gallery Forests (Cabrera, 1953). The latter is a vegetation of the Atlantic Forest. The Broadleaf Forest of the Parana and Uruguai rivers follow the baisns as far as the River Plate, but the composition of the associations changes along the soutward course of the rivers (Cabrera, 1953; Cabrera & Willink, 1973).

Scattered throughout the domain several meadows occur as enclaves. These formations are similar, in structure and composition, to the mixed prairies of Rio Grande do Sul and Uruguay. (Hueck, 1972; Klein, 1975).

The Mammal fauna is not well-known. An Andean Cricetid Rodent, Thomasomys occurs there. Vanzolini (1970) and Muller (1973) noticed that the region seem to not have a particular Vertebrate Fauna. The former author considers the region as an extension of the Atlantic Forest in faunistic terms. However, some Invertebrates seems to have links with the Araucaria Forest of the Andes (Muller, 1973) as some Coleptera for instance (Kuschel, 1960).

14. Andean Subtropical and Temperate Domain

This domain lies in Chile between 30° to 40° latitude south. The region has well-marked seasons, with dry summers and

rainy winters. In the coast, the rainfall is variable, some years having a long drought.

The domain includes the Araucaria araucana forest, in the middle altitudes. Another Conifer, Libocedrus is also a component of these forests. Above the Araucaria Forests, Notophagus ones exist. Woods with coriaceous leaves also occur in this region (Hueck, 1973). Apparently, there is no peculiar Fauna in this area (Cabrera & Willink, 1973; Muller, 1973).

15. The Coxillas (Subtropical Mixed Prairies Domain.

The region of the Pampas begins where the plains substitute the highlands in Southern Brazil. These Pampas, lying in the State of Rio Grande do Sul and Uruguay, are somewhat different from the Argentinian Pampas (Ab'Saber, 1971; 1977).

The rainfall is high (more than 1000mm/yr) throughout both the hot summers and the cold winters, and falls regularly on the characteristic types of prairie soils in the region (Queiroz Neto, 1968).

The typical vegetation, meadows, cover most of the area. The terrain is gently ondulated, low hills with the Coxillas (portuguese Coxilhas) being covered by the prairie (Ab'Saber, 1971) A gallery forest can be found in the troughs between the Coxilhas, as well as along the river banks. The vegetation of the gallery forests is composed of species from the highlands. A peculiar forest exists in the transitional zone of the La Plata delta. (Cabrera, 1953; Cerqueira, 1976). Araucaria does not follow these rivers and there is a progressive substitution of species. The domain is also the nuclear area of distribution of several species of Vertebrates (Muller, 1973; Ximenez et al., 1972). Some species occur in both

the Pampas and Coxilhas with a substitution of Fauna from south to north (Cerqueira, 1975; Languth & Abella, 1970).

16. Humid Pampa Domain

This region is similar to the Coxilhas, but the terrain is more plain. Under the influence of the Atlantic Polar front, the temperatures are lower and the humidity higher than the preceding domain.

There are extensive prairies with apparently no endemic species of trees (Hueck, 1973). The fertility of this soil turned the area into one of the most important wheat and beef cattle zones in the world. The Vertebrate Fauna is also distinc in that the region is the core area for the distribution of several species (Muller, 1973).

17. Domain of the Paramos

The Paramos are found in the Northern Andean altitudes above 3800m up to 4700m, where the snowline begins. In some places the lower limits lie at about 3000m.

The temperature is low, the weather instable, cloudy and rainy days alternating with the drier and brighter ones. The soil is deep with high content of water. However, the vegetation is xeromorphic, due to the reduced absorption caused by low temperatures and the high osmotic pressure of the soil.

These high altitude meadows have extensive grasslands wit scattered shrubs and cactuses. The vegetation is poorer and on poorer soil in the stepped slopes of the higher altitudes (Cuatrecasas, 1958).

Successive belts of vegetation with decreasing complexity and number of trees forms the transition from the rain forests of

lower altitudes. The inferior belts of the Paramos, the Subparamo, is a shrubby community with some trees scattered among the bush (Ab'Saber, 1977; Cuatrecasas, 1958).

According to Hershkovitz (1962; 1972), the Paramo does not have a Mammal Fauna of its own. The majority of Mammals reported in the domain seem to appear chiefly in the Subparamo, and although they wander through the Paramo, they do not stay there permanently. Other Vertebrates live in the Paramo itself and the Northern Andean Paramo Fauna has a barrier in southern Ecuador. However, some animals can be found beyond this point throughout the Peruvian Andes, where the Fauna must be considered transitional between the Puna and the Paramo (Muller, 1973).

Cabrera & Willink (1973) considered all high andes as a peculiar biogeographic province. The Paramo Domain includes the higher and stepped slopes of bare rocks, where the biota is characteristic. However, the biota of the same orography in the Puna region is different. These two domains may show resemblances, but although the Puna is a semiarid region, the Paramo is humid.

18. Domain of the Monte (with Cactaceae)

The Monte Desert has been divided into two parts on the basis of differentiated rainfall (Morello, 1958). However, the vegetation throughout the region seems to be uniform (Cabrera, 1953; Cabrera & Willink 1973; Hueck, 1972). The distribution of the rainfall is more significant than the total amount of rain. In the North, although,there is a rainy season in the summer, with up to nine months of drought (Mares, 1975).

The temperature lies between 14^{o} to 20^{o} and the rainfall

from 100mm to 350mm/year.

The vegetation is varied. According to Mares, (1975), "standing on an upper slope (which is almost invariably very steep) of a typical Northern Monte Valley, one would be amidst rocky hill sides covered by dune mats of Bromeliads and tall Cacti (Trichocereus, Cereus) in abundance. This grades rapidly at the base to a mixed-shrub community on the upper bajada and finally to the low (less than 2 meters) Laurea - dominated community of the lower bajada and flats. Gullies leading from the mountains cut into the valley in numerous locations and are populated by the tall tree and shrub community (Greater than 5 meters) consisting principally of Prosopis and Acacia. Generalizing, one can say that the tall forests of the Monte are limited to areas of permanent or semi permanent water."

Sandy dunes and salty faats must be added to the picture.

The Fauna of the Monte is partly shared with the Pampa and the Chaco (Muller, 1973) with elements also from the Puna (Hershkovitz, 1972; Mares, 1976; Blair et al., 1976). Some Patagonian elements also range through the Monte (Muller, 1973). However, South of Rio Negro, typical Monte animals are not to be found.

It is to be found that there are species with high degrees of adaptiveness to desert environments among the Caviamorph Rodents Othet Mammals are found in other open areas of the Continent, not being particularly adapted to arid landscapes (Mares, 1976).

19. Domain of the Stepped Monte

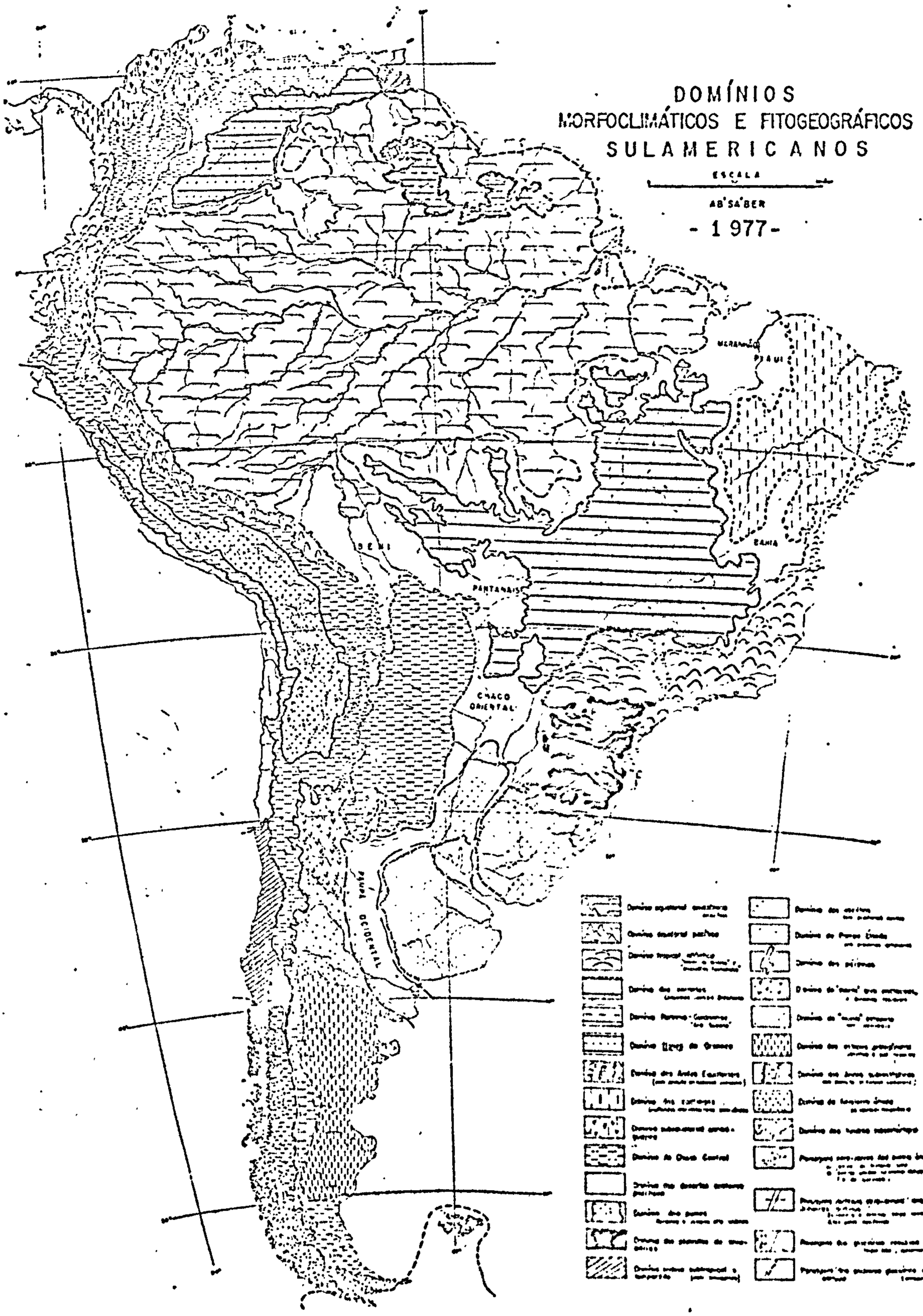
Ab'Saber,(1977), considers that the Southern Monte of Morello (1958) deserves to be considered as a distinc domain. In terms of rainfall and the climate in general, this seems to be correct. The climate is Mediterranean (Ab'Saber, 1977), but in relation

DOMÍNIOS MORFOCLIMÁTICOS E FITOGEOGRÁFICOS SULAMERICANOS

ESCALA

AB'SÁBER

- 1977 -



to the Monte, the vegetazion does not show such stricking differences in composition. However, the Monte itself may be described as a desert and the Southern Monte as a steppe.

The Fauna which characterizes the whole region has its core in the north (Muller, 1973).

A large belt of less humid Pampas, the Western Pampas, separates the Monte from the humid Pampa.

20. The Patagonia (Patagonian Domain)

South of the Monte, a large region of steppes and deserts extends to the Tierra del Fuego, limited in the west by the Andes. This region, the Patagonia does not have a high relief, showing intensive erosion, formed by plateaus, tafelbergs and extensive valleys. Rainfall and temperature are low, the former ranging between -19°C to +13°C , the average ranging to 5°C to 13°C. The rainfall ranges between 100mm/year to 300mm/year. Strong winds are very frequent.

The vegetation is shrub and grassland steppe. The Fauna shows a progressive impoverishment north to south. (Darlington, 1965).

21. Domain of the Subantartic Andes

In the southern Andes, there is no plains between the Mountains and the sea. The altitude is not high but there is a high content of atmospheric moisture, with consequent high rainfall and cloudness. The rainfall is lowered north to south.

The region has a very distinctive Flora and Fauna, being Notophagus its most well known Floral element (Cabrera & Willink, 1973; Darlington, 1965; Hueck, 1973). Large numbers of genera of animals and plants has links with the Australasian Region. Several authors

have considered this region distinct from the Neotropics, both in terms of Fauna (Haffter, 1964; Rapopo, 1965; Monros, 1958) and Flora (Cabrera & Willink, 1973). These latter authorities consider that a proper Biogeographic region, the Antartic Region, must be considered.

The Biota of the area have shown a complex zonation (Ab'Saber 1977) both altitudinal and latitudinal (Cabrera & Willink, 1973; Muller, 1973). Inger lakes and altitudinal glaciers are to be found (Ab'Saber, 1977).

22. Domain of the Subhumid Finisterra

The region is more cold than the previous one. It is also part of the Antartic Biogeographic Region. Notonhagus forests are characteristic. There is also an altitudinal and latitudinal zonation (Hueck, 1972).

23. Domain of the Subantartic Tundra

This domain also belongs to the Antartic Region. It is a humid, cold and cloudy region. Average temperature ranging around 5°C with low rainfall, 500mm to 700mm/year.

Notophagus exists only locally where the orography protects them from the winds. The forests are absent in the Falklands, South Georgia and other islands (Hueck, 1972). Tundra is the name which best fits the zone.

24. Intrazonal Humid Hills

Under the shadow of local mountains, a forest may develop In the Tucumano-Bolivian region and in the "Serra Humidas" and Brejos of Northeastern Brazil, this type of landscape is to be found.

The processes which cause the phenomenon have been discussed in the parts corresponding to the Caatinga and Atlantic forests.

In the foothill of the Andes in Northern Argentinan Andes, and Southern and Central Bolivia, a vegetation, with altitudinal zonation, has been characterized. The vegetation shows patterns which follow closely the orography and the distribution of rainfall (Fig.) Hueck, 1972). In the Caatinga enclaves, these landscapes occupy only somewhat small areas, some of these so small that in common vegetation maps they generally will not be cartographed.

25. Andean Rocky Landscapes

Intrazonally in the higher altitudes of stepped slopes, of Andes, rocky surfaces occur. Dry valleys, glaciers, etc. are common landscapes on the whole to Andean chains. Vegetation, when present, is xeromorphic and derived from the lower Puna and Paramos (Cuatrecasas, 1958; Weberbauer, 1945).

Between the higher parts of the mountains, the valleys show a barren facies due to the interception of the atmospheric moisture by higher mountains. These valleys show different facies locally (Hueck, 1972) (Fig.).

As a Whole, these landscapes do not constitute an h mogeneous domain, being, however, bearers of common features, all caused by the orography.

26. Landscapes of Residual Glaciers and the Finger Lakes in Southern America.

In the South of South America, the Glaciers occupie altitudes which in lower latitudes are filled with other kinds of

landscape (Domains 7,12, 17, and 25). The landform is dominated by the glaciers, with the characteristic finger lakes cocuring through the area.

27. Glacial Altitudinal Enclaves

In the higher altitudes of the Andes, including the Equatorial region, there are in the higher peaks of the mountains eternal ice, residuals of glacial landscapes.

APENDIX II

COLLECTING LOCALITIES: GAZETTEER

A - Didelphis albiventris group

ARGENTINA	
Cruz del Eje, Cordoba	30°44'S-64°45'W
Goya, Corrientes	29°10'S-59°15'W
Las Heras, Buenos Aires	not located
La Palmas, Corrientes	27°08'-58°45'
Los Ingleses, San Miguel,Bs.As.	34°40'-72°55'
Noetinger	not localted
"Tucuman"	
BRAZIL	
.Alagoas:	
Palmeira dos Indios	09°22'S-36°25'W
Quebrangulo	09°17'-36°30'
Vicosa	09°22'-36°14'
.Bahia:	
Barreiras	12°08'-44°59'
Bonfim	12°20'-45°10'
Feira de Santana	12°15'-38°57'
Jaguaquara	13°31'-39°58'
Jequie	13°51'-40°04'
Juazeiro	09°24'-40°30'
Lamarao	10°46'-40°21'
Palmeiras	12°30'-41°34'
Sao Goncalo	12°26'-38°56'
Seabra	12°25'-41°46'
Serrinha	11°39'-39°00'
Vitoria da Conquista	14°50'-40°50'
.Ceara:	
Baturite	04°20'-38°56'
Crato	07°13'-39°24'
Icarai, Mosquito	03°05'-39°38'
Ipu	04°19'-40°42'
Itapage	03°41'-39°35'
Missao Velha	07°14'-39°29'
Pacoti	04°13'-38°56'
Sao Benedito	04°03'-40°53'

.Goias:	
Anapolis	16°19'-48°58'
Aragarcas	15°55'-52°12'
Brasilia (Distrito Federal)	16°13'-44°29'
Caldas Novas	17°32'-48°37'
Cana Brava	09°14'-48°12'
Pocao	not located
Pouso Alto	12°00'-46°30'
.Mato Grosso:	
Ivinheima	22°10'-53°30'
Jacare, Alto Xingu	not localted
Maracaju	21°37'-55°12'
Sao Luiz de Caceres	16°05'-57°40'
Serra do Roncador	12°49'-51°46'
Serra da Chapada	15°26'-55°45'
.Minas Gerais:	
Belo Horizonte	19°55'-43°50'
Jequitinhonha	16°28'-41°01'
Jordao river, near Araguary	18°38'-48°73'
Lagoa Santa	19°36'-43°44'
Paraopeba	19°15'-44°24'
Passos	20°43'-46°36'
Pirapora	17°20'-44°57'
Pouso Alegre	22°14'-45°56'
.Paraiba:	
Princesa Isabel	07°44'-37°59'
.Pernambuco:	
Araripina	07°32'-40°34'
Bodoco	07°42'-39°53'
Bom Conselho	09°10'-36°37'
Exu	07°30'-39°43'
Garanhuns	08°53'-36°29'
Pedra	08°30'-36°53'
Pesqueira	08°21'-36°42'
Triunfo	07°51'-38°08'
.Rio Grande do Sul:	
Novo Hamburgo	29°41'-51°07'
Passo Fundo	28°15'-52°24'

Porto Alegre	30°02'S-51°13'W
"Rio Grande do Sul"	
Sao Lourenco	31°23'-52°04'
.Sao Paulo:	
Barrinha	21°12'-48°09'
Botucatu	22°52'-48°27'
Campestre,Morro do Lins	not located
Ourinhos	22°58'-49°52'
Presidente Epitacio	21°46'-52°06'
Ribeirao Preto	21°10'-47°48'

BOLIVIA

Cochabamba, Cochabamba	17°26'-66°10'
Incachaca, Cochabamba	not located
San Jose de Chiquitos	17°50'-61°00'

COLOMBIA

Bogota, Cundinamarca	04°38'N-74°65'W
Boqueron de San Francisco	(Bogota)
Rio Balcones	(Bogota)
San Adolfo, Huila	±1°42'-75°50'
San Antonio, Huila	±2° -76°
San Antonio, Valle	not located
Valdivia, Antioquia	07°10'-75°25'

ECUADOR

Baños, Tungurahua	01°26'S-78°24'W
Cuenca, Azuay	02°53'S-78°39'W
Guayllabamba, Riobamba	78°18'-00°02'S
Guapallo, Pichincha	00°11'S-78°30°W
Ibarra, Pichincha	00°21'N-78°07'W
Inaialabamba, Pichincha	±1°30'S-78°30'W
Loja, Loja	03°59'S-79°16'W
Quito, Pichincha	00°14'-78°30'W
Sig-Sig, Azuay	03°04'S-78°50'W

PARAGUAY

Chaco, Estancia La Urbana	not located

Chaco,Estancia La Geraldina	not located
Chaco,Estancia La Germania	not located
Nueva Germania, Chaco	23°52'S-56°44'
Pugua, Chaco	not located
Sapucay	not located

PERU

Corosha, Amazonas	not located
Chospyor, Rio Huarocondo	13°23'S-72°15'W
Macchu Picchu, Cuzco	13°08'S-72°30'W
Ocabamba, Cuzco	13°32'S-71°57'W
Ocaneque, Puno	±14° S-69° W
Oceledin	±7° S-76° W
Porontoy	not located
San Mateo	03°46'-71°30°
Surca, Lima	not located
Taulis(Hacienda), Cajamarca	not located
Vera Mayo	not located
Yanamayo	not located
Acora	15°59'S-69°48'W
Callao, Lima	12°05'S-77°08'W

B - Didelphis marsupialis group

ANTILLAS

Grenada

St. Vincent

St. Lucia

Dominica

ARGENTINA

"Missiones"

BOLIVIA

Buenavista, Santa Cruz	17°28'-63°37'
Chapare,river, Cochabamba	
Chulumani, La Paz	16°22'-67°30'

Mapiria, La Paz	15°16'-68°14'
Astillera	not located

BRAZIL

.Amapa:	
Amapa	02°03'N-50°47'W
Calcoene	02°29'-50°57'
Mazagao	00°10'S-51°16'W
Rio Maraca	(Mazagao)
Rio Maruanum	not located
Vila Velha do Cacipore	03°20'N-51°20'W
Terezinha	
Serra do Navio	00°59'N-51°50'W
.Alagoas:	
Mangabeiras, Usina Sinimbu	(Sao Miguel dos Campos)
Sao Miguel dos Campos	09°46'S-36°05'W
.Amazonas:	
Itacoatiara	03°08'S-58°25'W
Manaus	03°08'S-60°01'W
Tapuniquara	not located
.Bahia	
Bahia, The Reconcava	probably Salvador
Ilheus	14°47'-39°02'
Itaparica	12°52'-38°45'
.Espirito Santo	
Campinho	
Engenheiro Reeve	20°46'-41°29'
Morro de Argolas	20°20'-40°20'
Santa Tereza	19°56'-40°36'
Serra	20°07'-40°18'
Vila Velha	20°23'-40°18'
.Maranhao	
Anil	01°40'S-45°19'W
.Mato Grosso	
Serra do Roncador	12°49'-51°46'

.Minas Gerais:	
Alem Paraiba	21°52'-42°40'
Caete	19°53'-43°39'
Itumirim	21°19'-44°53'
Juiz de Fora	21°45'-43°20'
Pocos de Caldas	21°50'-46°33'
Teofilo Otoni	17°51'-41°30'
Volta Grande	21°46'-42°32'
.Para:	
Anandeva	01°22'S-48°28'W
Belem	01°28'S-48°29'W
Braganca	01°03'S-46°45'W
Caldeirao	00°35'S-51°03'W
Cameta	02°14'S-49°29'W
Castanhal	01°17'S-47°55'W
Caxiriatuba	02°36'S-54°56' W
Chaves	00°10'S-49°58'W
Curralinho	01°48'S-49°48'W
Ipitinga, Rio Acara	not located
Itaituba	04°26'S-55°59'
Lazaropolis do Prata	not located
Mexiana	00°00' -49°30'W
Obidos	01°55'S-55°31'W
Pau de Letra	(Near Santarem)
Piquiatuba	02°40'S-54°58'W
Rio Abaete	not located
Sao Miguel do Guama	01°42'S-47°23'W
Santarem	02°26'S-54°41'W
Tapereba	(see Chaves)
Taperinha	02°30'S-54°20'W
Timboteua	01°11'S-47°10'W
Utinga	(see Belem)
.Rio de Janeiro:	
Casimiro de Abreu	22°28'-42°12'
Duque de Caxias	22°47'-43°19'
Mangaratiba	22°57'-44°02'

Rio (Floresta da Tijuca)	22°53'-43°12'
Sao Joao Marcos	22°30'-44°05'
Terezopolis	22°26'-42°58'
Serra da Carioca	(The same range as Rio)
Tingua, Nova Iguacu	22°45'-43°26'
.Roraima (ex Rio Branco)	
Boa Vista	02°48'N-60°42'W
Santa Catarina	
Hansa	(not located, probably at Vale do Itajai)
Humboldt	(see Hansa)
Joinville	26°20'-48°49'
.Sao Paulo	
Bertioga	
Boraceia	
Cacapava	23°06'-45°42'
Caraguatatuba	22°39'-45°26'
Cotia	23°35'-46°55'
Cruzeiro	22°34'-44°57'
Ipiranga	not located
Itatiba	22°59'-46°51'
Ituverava	20°22'-47°48'
Lins	21°45'-49°45'
Piquete	22°37'-45°10'
Pirituba	not located
Sao Sebastiao	23°49'-45°25'
Taubate	23°02'-45°34'
Ypanema	23°26'-47°36'

COLOMBIA

Antioquia, Antioquia	06°36'N-75°53'W
Cali	03°24'N-76°36W
Charguayco, Cauca	not located
Concordia, Medelin	06°03'N-75°57'W
Maipures, Orinoco River	05°17'N-67°51'W
Munchique, Cauca	not located

Pamplona, Santander	07°24'N-72°38'W
Popayan, Cauca	02°27'N-76°22'W
Rio Arauca, Arauca	not exactly located
Rio Cobaria, Arauca	not exactly located
Sabaneta, Cauca	not located
San Cristobal	not located
San Juan Nepomuceno	± 9° N-75°W
San Sebastian, Magdalena	10°37'N-73°34'W
Santa Marta	11°18'N-74°10'W
Socorre, Bolivar	08°00'N-76°04'W
Sonson, Antioquia	05°42'N-75°17'W
Tres Troncos, Caqueta	00°08'N-74°41'W
Unguia, Antioquia	08°00'N-77°04'W
Uraba, Antioquia	not exactly located
Valdivia, Antioquia	07°10'N-75°25'W
Villavicencio, Meta	04°09'N-73°38'W
ECUADOR	
Guayaquil, Guaias	02°13S-79°54'W
Jambilar	not located
"West of Ecuador"	
Ancon, Guayas	02°18'S-80°42'W
Anayaquil	not located
Babahayo, Pinocha	01°53'S-79°40'W
GUIANA	
Supinaam River	06°58'-58°31'
Demerara	06°48'-58°11'
Bartica Grove	06°24'-58°38'
Kanuku Mountains	
Makenaam, Essequibo	not located
GUYENNE FRANCAISE	
Cayenne	04°55'-52°18'
PARAGUAY	
Caaguazu	25°35'-56°05'

PERU	
Pacasmayao	07°27'S-79°33'W
Eten, Piura	06°55'S-79°50'W
Rique, Lambayque (Lambayaque)	06°36'S-79°45'W
Piura	05°15'S-80°38'W
Huampami, Amazonas	not located
Huaynapata, Marcapata	not located
"Junin"	
"Marcapata"	
San Nicolas, Amazonas	03°37'S-71°36'W
SURINAM	
Bigi Santi	06°02'-55°21'
Camp I	not located
Copiweg	06°24'-55°16'
Coronie	05°50'-56°16'
Kasabaholo kreek	(7 km SW Paramaribo)
Lucie River	
Niew Amsterdam	06°08'-55°10'
Paramaribo	05°52'-55°14'
Sipaliwini (airstrip)	02°01'-56°06'
Wageningen	06°14'-57°23'
Vitkijk	06°19'-55°16'
Zanderig	05°21'-55°19'
TRINIDAD	
	10°40'-61°31'
VENEZUELA	
Cumana, Sucre	10°27'-64°10'
Kasmera, Zulia	(37 km WSW Machiques)
Maracay, Aragua	10°15'-07°35'
Motopan, Trujillo	not exactly located
Nucleo El Laurel, Miranda	not exactly located
Rancho Grande, Aragua	not exaclty located
San Esteban	not located

APENDIX III

MATERIAL EXAMINED

A - Didelphis albiventris group

ARGENTINA

Buenos Aires: Buenos Aires (including Los Ingleses)-BM9.12.1.51; BM9.12.1.53;BM9.12.1.52;BM20.2.7.39;BM17.1.25.57;BM9.12.1.55;BM17.1.25.56;MN23691/Las Palmas-ZSM 1 not listed.

Cordoba:Cruz del Eje-BM2.2.5.38;BM17.1.25.58;BM17.1.25.59/Noetinger - BM17.1.25.60

Corrientes:Goya-BM98.8.19.1; BM 4 not listed here.

Missiones:unspecified-ZSM1926/130/Dos de Maio-ZSM1960/55;ZSM1966/55.

Tucuman:Cerro del Campo(Bunayecer)-BM26.2.13.166/MalahalaBM6.3.23/unspecified: BM 3 not listed.

BOLIVIA

Cochabamba:Chapare-ZSM1954/316;ZSM1954/317 plus BM 3 not listed/Incachaca-BM 1 not listed.

La Paz:Chulumani BM 1 not listed.

Santa Cruz: San Jose de Chiquitos-ZSM1925/626;ZSM1925/627;ZSM1925/628

COLOMBIA

Antioquia:Valdivia FM69807; BM 1 not listed

Cauca:Cauca-FM88461

Cundinamarca:Bogota(including Boqueron)-FM70779;FM70777;FM70780;FM70781;FM70776;FM70778;MP 1920/98; BM 7 not listed here.

Huilla:San Adolfo-FM70785;BM 1 not listed/San Antonio:FM70770;FM70772;70773;FM70774;BM 4 not listed.

Valle:San Antonio-MVZ124028;MVZ124029

ECUADOR

Azuay:Cuenca- BM 5 not listed/SigSig- BM 3 not listed here.

Pichincha:Cayambe- BM 2 not listed/Gnapallo BM 1 not listed/Ibarra- BM 2 not listed/Quito- BM 3 not listed.

Loja: Loja- BM 1 not listed

Riobamba: Inaialabamba- BM 3 not listed here.

PARAGUAY

Chaco (including La Urbana, La Germania, Nueva Germania and La Geraldina):ZSM(all numbers)-1925/630;1926/393;1926/394;1926/395;1926/398;1926/400;1925/622;1925/623;1925/624;1925/629;1931/258;1931/260;1931/263;1931/264.

PERU

Cajamarca:Hacienda Taulis-MVZ12171;MVZ12170.

Cuzco:Ocabamba-MVZ152834/Macchu Picchu- BM 1 not listed.

Lima:Callao- BM 2 not listed/Surca-BM 1 not listed here.

Amazonas:Corosha-MVZ139956.

Puno:Ocaneque(near Limbani)-MVZ116040

Other localities undetermined in British Museum: Acoria- 1BM/ Chospyor-BM 1/Oceledin- BM 1/Porontoy- BM 1/San Mateo- BM 1/ Vera Mayo- BM 1/Yanamayo- BM 1.

Venezuela - Merida ($08^{o}35'N-71^{o}09'$) - BM 1

BRAZIL

Alagoas:Palmeira dos Indios-MN22873;MN23578;MN23579;MN22874; MN22875;MN22876;MN22877;MN23746;MN22805;MN23747;MN23744;MN 23584/Quebrangulo-MN22883;MN22880;MN22879;MN22878;MN22884/ Vicosa-MN22885;MN22882;MN22881

Bahia: Barreira-MN4248;MN4254;MN4253/Bonfim-10023MN/Feira de Santana-MN23633;MN22892;MN17236;MN22888;MN17202;MN8322;MN22889;MN 22895;MN17201;MN22890;MN22891;MN22893;MN17199;MN17200;MN17237; MN17247;MN22894;MN17237;MN22897;MN22900;MN22921;MN22902;MN22909; MN22911;MN22914;MN22917/Jaguaquara-MN17225;MN22925;MN22926;MN 17226;MN17238;MN17246;MN17244;MN172232;MN22925;MN22922;MN22923; MN22924;MN17227/Jequie-MN22927;MN22926/Juazeiro-MN4251;MN4255/ Lamarao- BH 2 not listed/Palmeiras-MN22936/Sao Goncalo-MN 2 not listed/Seabra-MN22919;MN22933;MN22934;MN22935;MN22939;MN22941 ; MN22929;MN22937;MN22938;MN22940/Serrinha-MN22948;MN22945; MN 22953;MN22952;MN22947;MN22951;MN22954;MN23689;MN22944;MN22942; MN22945;MN22946;MN22943/Vitoria da Conquista-MN8322/Vila Nova - MZ2603;MZ2605. More Feira de Santana-MN22915;MN22916;MN22917; MN22918;MN22920;MN22909;MN22911;MN22914;MN22908;MN22905;MN22910; MN22913;MN22912;MN22898;MN22896;MN22899;MN22900;MN22897;MN22902; MN22921;MN22903;MN22901;MN22904.

Ceara:Baturite-MZ8698;MZ8699;MZ8700/Crato-MN23605;MN23603;MN23602 ;MN17214;MN17250;MN23613;MN23619;MN23601;MN23521;MN23608;MN23610; MN23615;MN23612;MN23618;MN23607;MN23609;MN23611;MN23620;MN23617; MN23599;MN23606;MN17254;MN23592;MN23596;MN23598;MN23591;MN23597; MN23594;MN6733;MN23593;MN23590;MN23595;MN17253;MN17249;MN17212;MN 17251;MN17206;MN17210;MN17208;MN17213;MN17215;MN17209;MN17207 ;

MN17252;MN17248;MN17211;_MN23614;MN23616;MN23629;MN17259;MN23623;
MN22631;MN17258;MN23627;MN17265;MN23604;MN23644;MN17269;MN17255;
MN17267:MN17256;MN17262;MN17261;MN17263;MN17268;MN17260;MN17257;
MN17205;MN23543;MN23541;MN23544;MN23539;MN23540;MN23542;MN23550;
MN23551;MN23549;MN23547;MN23546;MN23545;MN23548/Icarai(Nosquito)
-MZ8701/Ipu-MN23630;MN17203/Itapage- MN 1 not listed/Missao Ve-
lha-MN23626/Pacoti-MN 1 not listed/Sao Benedito-MN23630.
Goias:Anapolis-MN4545;MN5093;MN4559;MN4563;MN4614;MN4742;MN4748;
MN4756;MN4741;MN4763;MN4725;MN4741;MN20959;MN20961;MN4691;MN4740;
MN4751;MN4743;MN5092;MN4501;MN4561;MN4518;MN5094;MN4520;MN4547 ;
MN5096;MN4615;MN4557;MN4519;MN5100;MN5097;MN4558;MN4546;MN5095;
MN4590;MN4589;MN5101;MN4550;MN4663;MN4567;MN4568;MN5093;MN4566;
MN4552;MN4720;MN4521;MN4562;MN4759;MN4747;MN4735;MN4746;MN4438;
MN4752;MN4755;MN4734;MN4750;MN4494;MN4737;MN4758;MN4739;MN4488;
MN4754;MN4491;MN4496;MN4736;MG1725 /Aragarcas-MG2408;MG 1479 ;
MG1625/Brasilia(Distrito Federal)-MN22248;MN22252;MN2250;MN22253;
MN22254;MN22251;MN22230;MN22249/Caldas Novas- MN 1 not listed /
Cana Brava-MZ4098;MZ4133;MZ4134/Pocao-MN1502/Pouso Alto- MN 8
not listed.
Mato Grosso:Ivinheima-ZSM1938/254 /Maracaju-MN4493;MN4486;MN4549;
MN4553;MN4554;MN4564;MN4645;MN4692;MN4626;MN4629;MN4497;MN4499;
MN4760/Sao Domingos,Rio das Mortes-MZ7039/Sao Luiz de Caceres-
MN1193/Serra do Roncador - BM 1 not listed/Serra da Chapada-
BM 4 not listed.
Minas Gerais:Belo Horizonte-BM 4 not listed/Jequitinhonha,Rio -
BM 1 not listed/ Jordao, Rio (near Araguari)-BM 1 not listed/
Lagoa Santa-MN4229;MN13414;MZ4096;BM 2 not listed/Paraopeba -
MN 1 not listed/Passos-MN22979;MN22966;MN22982;MN22976;MN22978;
MN22970;MN22975;MN22980;MN22974;MN22972;MN22981;MN22961;MN23641;
MN22959;MN20956;MN22957;MN22956;MN23637;MN22965;MN23634;MN23636;
MN23638;MN22964;MN22962;MN23635;MN23639;MN23640;MN23642;MN20956;
MN22957;22960MN;MN22968/ Pirapora-MN4289;MN22973;MN22968;MN4290;
MN13414;MN22967;MN22969;MN22977.
Paraiba: Princesa Isabel-MN22862;MN22860;MN23579/Mamamguape-MZ
8452. MN22869
Pernambuco: Araripina (see among Bodoco)/Bodoco-MN23564;MN23685;
MN17266;MN23562;MN23563;MN23684;MN23566;MN23682;MN23683;MN23565/

Bom Conselho-MN23695;MN23589;MN23588;MN23587;MN23586/Exu- MN 1 not listed/Garanhuns-MN23651;MN23652;MN23572;MN17224;MN23561;MN23670; MN23585;MN23669;MN23751;MN23671;MN23672;MN23559;MN23676;MN23677; MN23673;MN23675;MN17221;MN23653;MN23680;MN23560;MN23667;MN23678; MN23666;MN23687;MN23554;MN17241;MN23645;MN23643;MN23647;MN17218; MN17245;MN23688;MN17220;MN23552;MN17240;MN23649;MN23646;MN17243; MN23648;MN23558;MN23668;MN23679;MN23654;MN23674/Pedra-MN17239 / Pesqueira-MN23696;MN23694;23588MN;MN23587/Triunfo-MN23572;MN23574; MN23575;MN23576;MN23578;MN23577;MN23573;MN23567;MN23579;MN23571; MN23568;MN23570;MN23697;MN23698;MN23699;MN23583;MN22857;MN22864; MN22867;MN22866;MN22865;MN22871.

Rio Grande do Sul: Novo Hamburgo- MN 1 not listed/Passo Fundo-ZSM 1 not litsed/Porto Alegre- MN 1 not listed/"Rio Grande do Sul"- BM 2 not listed/Sao Lourenco-MZ1653;MZ1650:MZ1656;MZ1652;MZ 115; MZ2041;MZ2033;MZ2338;MZ241;MZ2047;MZ108;MZ2048;MZ2339;MZ83;MZ88.

Sao Paulo: Barrinha-MN 1 not listed/Campestre-MZ6167;MZ6168;MZ 6170;MZ6169/Ourinhos-MN23735/Presidente Epitacio-MZ3717;MZ3716; MZ3779/Ribeirao Preto-MZ10363;MZ7138;MZ10361;MZ10362/Itapetininga -MZ10122;MZ10123;MZ10131;MZ10133;MZ10137MZ10028;MZ10124;MX10126; MZ10227;MZ10129;MZ10132;MZ10130;MZ10134;MZ10135;MZ10136;MZ10029.

B - Didelphis marsupialis group

B1- Didelphis aurita

BRAZIL

Alagoas: Sao Miguel dos Campos- MZ7366;MZ7606.

Bahia: Bahia (probably Salvador)- BM 3 not listed/Ilheus-MN11314; MN11307;MN11309;;MN11318;MN11319;MN11317;MN11328;MN11327;MN11325; MN11437;MN11330;MN11323;MN11324;MN11438;MN11419;MN11424;MN11426; MN11430;MN11435;MN11441;MN11445;MN11446;MN11447;MN11450/Itaparica - BM 1 not listed

Espirito Santo:Campinho-MN23758/Engenheiro Reeve-BM 1 not listed; Morro de Argolas-MN20948;MN3857/Santa Tereza-MN20947;MN5720;MN 5718;MN5892;MN5702/Serra-MN11671/Vila Velha-20946MN.

Minas Gerais:Alem Paraiba-MN3850;MN3859;MN20940;MN20943;MN3853; MN5641;MN7722;MN7721;MN3852;MN5700;MN5732;MN5744;MN20745;MN 20944;MN7624;MN7631/Caete-MZ47/Itumirim- MN 1 not listed/

Juiz de Fora:MN20939;MN20940;MN20941MN20938/Pocos de Caldas - MN23748;MN23749/Teofilo Otoni-MZ2731/Volta Grande-MN3851.
Rio de Janeiro:Casimiro de Abreu-MN23721/Duque de Caxias-MN5808; MN5796;MN3793;MN5795;MN5856;MN5811;MN5812;MN5792;MN5813/Mangaratiba-MN3854;MN3858;MN20950MN5739/Floresta da Tijuca (including Serra daCarioca and Morro do Amorim)-MN5862;MN6456;MN6457;MN10484 ; MN10489;MN5614;MN10482;MN10486;MN10488;MN10490;MN10491;MN10503; MN5688;MN5740;MN10483;MN5615;MN10485/Sao Joao Marcos-MN3856; MN5754/Terezopolis-Bm34.1.17.6;BM34.1.17.7;ZSM1937/188;ZSM MN7149;MN7150;MN7151;MN7152;MN7155;MN7154;MN7156;MN7157;MN7160; MN7163;MN7164;MN7165;MN7166;MN7167;MN7169;MN7172;MN7171;MN7175; MN7177;MN7180;MN7146;MN7159;MN7147;MN7148;MN7153;MN7158;MN7161; MN7170;MN7176;MN7178;MN7181;MN7179;MN20949/Tingua- MN 4 not listed/Itaguai (Baixada Fluminense)- ALP-1556;ALP-1158;ALP-1474; ALP-1157;ALP-2177.
Santa Catarina:Hansa-BM28.19.11.56;BM28.10.11.55;BM28.10.11.54; BM3.7.1.106/Humboldt-BM14.5.9.21;BM14.5.9.22;MB14.5.9.21;EM14. 5.9.22/Joinville-BM22.5.29.13;BM22.5.13;MZ1680;MZ1681;MZ
Sao Paulo:Bertioga-MZ9663;MZ10053;MZ9711/Boraceia-MZ9650;MZ9651; MZ9706;MZ9643;MZ9644;MZ10359;MZ9649;MZ10023/Caraguatatuba- MZ 9786/Cotia-MZ3016;MZ9699;MZ9700;MZ9701;MZ9702;MZ9703;MZ09709; MZ9923;MZ9911MZ10047;MZ10045;MZ10052;MZ10051;MZ10050;MZ9704 ; MZ9710;MZ9791;MZ9781;MZ9792;MZ9656;MZ9659;MZ9842;MZ10048;MZ 10049;MZ10046;MZ10044;MZ10055;MZ10054;MZ10056/Cruzeiro- BM1.2.7.61 ;BM1.2.7.55;BM1.2.7.56;BM1.2.7.57;BM1.2.7.62/Itatiba-MZ3708/Ituverava-MZ2991;MZ2989;MZ2990/Lins-MZ6164/Cacapava-MN23730/Piquete - BM1.6.690/Pirituba-MZ7789;MZ9790/Sao Sebastiao-MZ44/Taubate-MN 23732;MN23733/Ypanema-BM3.7.1.196;BM3.7.4.108;MZ19;MZ24.
Parana:Roca Nova-BM3.7.1.106;ZSM1901/116/Serrinha-ZSM1938/250 ; ZSM1938/237;ZSM1938/241;ZSM1938/238;ZSM1938/242.

B2 - Didelphis marsupialis s.s.

ANTILLAS

Dominica:Bm92.9.8.1.

Grenada:BM4.6.3.11

St. Lucia:BM1970.79

St. Vincent:BM91.5.15.6

BOLIVIA

Santa Cruz:Buenavista-BM28.2.75;BM28.2.77;BM28.2.9.78
Cochabamba: BM 3 not listed/Rio Chapare- BM 3 not listed here/
Incachaca-Bm 1 not listed.
La Paz: Mapiria- BM 4 not listed/Chulumani- BM 1 not listed.
Astillera (unprecise locality) - BM 1 not listed.

COLOMBIA

Antioquia:Antioquia-FM69571;FM69810;FM69572/Sonson-MP1929/665;
1929/666;1929/668/Valdivia-FM69808/Unguia-FM69569;FM69570.
Arauca:Rio Arauca-FM92291;FM92293/Rio Cobaria-FM92289;FM92290;
FM92292;FM92294
Bolivar:San Juan Nepomuceno-FM68936/Socorre-FM68934;FM68935.
Caqueta: Tres Troncos-FM70787
Cauca:Charguayaco-FM86754;Fm86756;FM88466;FM89218;FM89219/Rio
Saija-FM90103;FM90065/Sabaneta-FM86755/FM88467/FM89365
Huila:Villavieja-MVZ113841;MVZ113368
Magdalena:San Sebastian (Serra Nevada de Santa Marta)FM69573/
Santa Marta-FM70786
Meta-Villavicencio-MVZ106222
Cauca:Popayan-FM85799;FM86753;FM86853/Munchique-FM88461;FM88463;
FM88464;FM88465
Santander:Pamplona-FM92288

ECUADOR

Guayas-BM99.8.1.49;BM99.8.1.18;BM58.459-Guayaquil/Ancon-BM 1 not
listed
Pinocha:Babahayo-MP1932/3000;1932/3002;1932/3001;1932/3003
Occidente:Mindo-MP1932/2863
Undetermined localities:Anayaquil-BM 1 not listed/San Javier-BM
1 not listed/Jambilar-BM1.6.5.17

GUIANA

Supinam river- BM 4 not listed/Demerara river- BM 1 not listed/
Essequibo(Bartica Grove)-BM 4 not listed/Kanuku Mountains- BM
1.6.4.125;BM1.6.4.126/Makenaam, Eseequibo- BM 1 not listed.

GUYENNE FRANCAISE

Cayenne-3.4.5.46;MP1902/54;MP1901/889/"Guyenne"-1972/631

PERU

Amazonas:Huampami-MVZ153303;MVZ153303;MVZ153305/San Nicolas- BM 26.10.15.30

Lambayaque: Rique (Eten)-BMO.3.1.87;BMO.3.1.98;BM 0.3.1.83; BM 0.3.1.84;BMO.3.1.85

Other Localities with samples in teh British Museum: Causrichupa (1)/Chancamayo(2);Huaynapata (1)/Junin (1)/Marcapata (1)/Pacasmayo (1)/Piura (1) (number of specimens examined in brackets)

SURINAM

Bigi Santi-LM23955/Coppieweg-LM177782;LM22177;LM22113/Coronie-LM 22118/Kasabaholo kreek-LM16165/Lucie River-LM18012/Niew Amsterdam -LM22123/Paramaribo-LM17763;LM12852;LM22122;LM17747;LM17791;LM 24026;LM22124;LM10789;LM8;LM21726:LM17762;LM17775;LM17802;LM22116; LM17803;LM22119;LM22115;LM24027;LM22125;LM22114;LM24028/Sipaliwini -LM17750/Wageningen-LM22553/UItikjk-LM17746/Zanderig-22117LM plus BM 2 not listed

TRINIDAD

BM 97.6.7.18 plus 3 not listed

VENEZUELA

Aragua:Maracay-ZSM1929/262;ZSM1929/263;ZSM1928/450/Rancho Grande-KU120270;KU120271;KU120272;KU120273;KU120274;KU120275;KU120276; KU120277;KU120278;KU120279;KU120280;KU120281;KU120281;KU120282; KU120283;KU120284

Miranda: Nucleo El Laurel-KU120231

Sucre:Cumana-KU117940

Trujillo:Motopan-KU120227;KU120228;KU120229

Zulia: Kasmera (Near Machiques)-KU120230

San Esteban (undetermined)-BM11.5.25.69

BRAZIL

Amapa:Serra do Navio-MN20057;MN200111;MN20103;MN20124;MN20128; MN20159;MN20053;MN20074;MN20086;MN20087;MN20089;MN20090;MN20092; MN20110;MN20106;MN20139;MN20153;MG8090;MG8512/Terezinha-MN20072; MN20088;MN20091;MN20093;20098/Mazagao-MG2271/Vila Velha do Cacipore-MG2273;MG2270;MG2272/Calcoene-MG68618/Amapa- MN 6 not listed

Amazonas-Itacoatiara-MZ4772/Manaus-MN20924;MN20963;MZ361;MN20922;
MN20921
Mato Grosso:Jacare,Alto Xingu-MN23750/Serra do Roncador-EH 1 not
listed
Para:Caxirituba-MZ4779/Caldeirao-BM23.8.10.27;BM23.8.10.28;BM23.
8.10.29;BM23.8.10.30;BM23.8.10.28.2;BM23.8.10.26/Mexiana-ZSH1910/
289;1910/291;1910/292/Curralinho-MN4503;MN4571;MN4940;MN4578;MN
4514;MN4505;MN4504;MN4532;MN4502;MN4570;MN20955;MN4533;MN4535;
MN4510;MN4511;MN4512/Chaves-MG1786;MG1790;MG1800;MG1785;MG1796/
Nova Timboteua-MN20953/Guama-MG1603;MG1752MG1596;Belem-MG689;
MG1405;MG1406;MG2543;MN1164;MN1165;MG976;MG977;MZ1192;MZ1749;
MZ2536;MZ410/Anandeua-MZ8558;MZ8560;MZ8559;MZ8561;MZ8563/Came-
ta-MZ4784/Itaituba-MG8614;MG8626;MG8606;MG8627;MG8607;MG8630;
MG8609;MN8625;MN8631;MN8623;MN8608;MN8624;MN8610;MN8612/Taperi-
nha-MG336;MG3367;MG3364;MG3373;MG3374;MG3363;MG3368;MG3372;MG
3371;MG3357;MG3370;MG3369;MG3362/Santarem-MG8506;MG8507;MG3361;
MG8510;MG8507/Pau de Letra-MZ4743/Braganca-MG1753/Lazaropolis
do Prata-MG2544;MG2540/Castanhal-MG2537;MG2539;MG2538;MG2537/
Caxiriatuba-MZ4768/MZ4788/Piquiatuba-MZ7335;MZ4770/Cameta-MZ
4747
Maranhao: Anil-MN1166
Roraima:Boa Vista-MG1750

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APENDIX IV

DISCRIMINANT ANALYSIS

DISCRIMINANT ANALYSIS

A discriminant analysis was performed between sets formed by the pooling of samples. Four sets were construed: Males, Eastern Brazil; Males, Northern South America;Females Eastern Brazil and Females, Northern South America. These sets were considered in the analysis two by two, but they were tested as well not considering the sexes. Both analysis gave satisfactory resulst.

Here are presented the means and standard deviation of each set. As a summary histograms based on the descriminant functions of each sexes is presented. The discriminant analysis seems to support the assertion made in chapters four and five that the black eared opssums are probably divided between two species in South America.

Means and Standard Deviations:

GROUP MEANS — Males - Subfiles = Sets: 1-Eastern Brazil;2-North South America

SUBFILE	GLS	GW	PL	A	IC	CDP	LAN	BAM
1	107.85096	102.66508	62.83784	57.10097	22.43137	11.30490	20.24611	30.81271
2	105.43376	102.90769	62.06906	54.81874	21.17968	11.40625	19.81876	30.61901
TOTAL	106.94210	102.88160	62.52108	56.22108	21.54479	11.34394	20.00301	30.80961

SUBFILE	MAC	BPS	MAX	SM	MAS	GUN	MAN	MAP
1	28.91000	17.59313	42.32150	19.21500	27.17254	15.94607	32.60307	50.66021
2	28.00150	17.29210	42.09063	19.30468	27.68749	15.72612	40.53201	50.00701
TOTAL	28.53782	17.47710	42.05120	19.24999	27.37108	15.86204	30.78975	50.42101

SUBFILE	MAD	SIM
1	86.20725	21.78725
2	84.99062	22.17343
TOTAL	85.70837	21.93614

GROUP STANDARD DEVIATIONS

SUBFILE	GLS	GW	PL	A	IC	CDP	LAN	BAM
1	4.11056	3.23524	3.90655	5.28156	2.86745	0.46231	1.91856	3.10036
2	3.37177	3.17141	2.89882	4.88833	2.89362	0.54006	1.86276	3.33654
TOTAL	3.91348	3.20533	3.56302	5.22406	2.59709	0.50699	1.91709	3.24652

SUBFILE	MAC	BPS	MAX	SM	MOS	GUN	MAN	MAP
1	2.33773	0.87556	1.36767	0.70324	3.17606	2.07367	4.76011	2.91791
2	1.83253	1.02920	2.23127	0.74526	2.69102	1.33099	4.62939	3.05665
TOTAL	2.10152	0.94321	1.77772	0.71653	2.97538	1.81953	4.74099	2.95067

SUBFILE	MAD	SIM
1	4.52612	0.83743
2	4.93731	0.89014
TOTAL	4.67249	0.87511

Females - Sets: 1-Eastern Brazil; 2-Northern South America

GROUP MEANS

SUBFILE	GLS	CW	PL	Z	IC	COP	CAN	BAN
1	95.000805	93.81944	53.72499	48.67360	18.80750	11.69167	17.01944	29.333334
2	100.83333	99.63456	62.34000	51.15000	20.43833	11.83000	18.02499	30.946000
TOTAL	98.04318	96.87181	60.23484	49.79924	19.59242	11.63636	17.74924	30.17575

SUBFILE	UAC	UPS	MAX	SN	ROS	GBN	NAS	MAP
1	25.81811	17.58749	40.13035	18.80416	24.97499	14.22917	46.30194	30.33139
2	26.79499	17.78160	41.31833	19.37333	27.77333	12.83000	48.04166	27.533999
TOTAL	26.27190	17.67575	40.67045	19.06287	26.02078	14.59318	47.15900	30.05000

SUBFILE	MAU	SIM
1	77.69305	21.51527
2	82.61033	22.31160
TOTAL	79.93181	21.87727

GROUP STANDARD DEVIATIONS

SUBFILE	GLS	CW	PL	Z	IC	COP	CAN	BAN
1	5.81414	5.87017	3.85224	3.61496	1.27012	0.53490	1.42319	1.26180
2	5.94393	5.54401	3.25693	3.32452	1.39232	0.64069	1.22751	1.30355
TOTAL	6.04092	5.34378	3.68250	3.07474	1.52939	0.56911	1.55305	1.45864

SUBFILE	UAC	UPS	MAX	SN	ROS	GBN	NAS	MAP
1	1.57949	1.03312	2.00160	0.93636	1.72664	1.60493	2.67927	1.31499
2	1.75342	1.00400	1.52210	0.79716	1.66240	1.52152	2.53741	1.44187
TOTAL	1.71326	1.01709	1.82927	0.91497	2.33875	1.58055	2.67039	1.40776

SUBFILE	MAU	SIM
1	5.00205	0.65587
2	4.93862	1.30752
TOTAL	5.53257	1.18928

SYMBOLS USED IN PLOTS

SYMBOL	GROUP	LABEL
1	1	SUBFILE MEST
2	2	SUBFILE MAJR

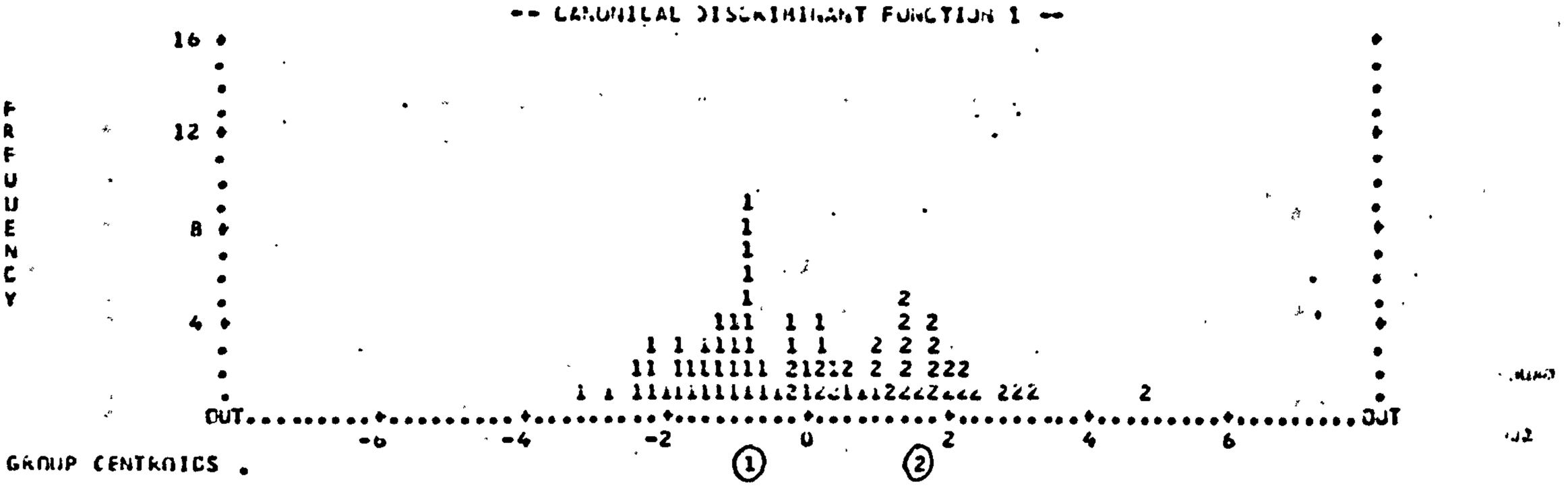
Group 1 - D. aurita ♂♂

Group 2 - D. marsupialis ♂♂

DISCRIMINANT ANALYSIS

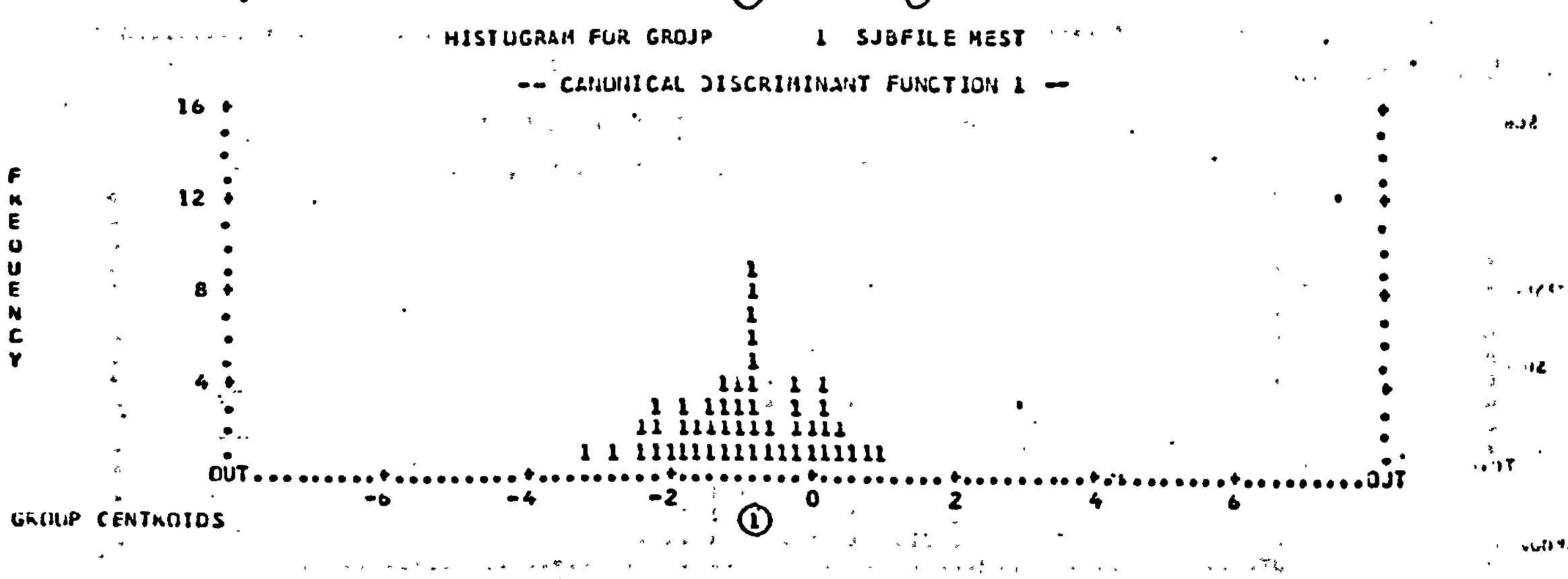
ALL-GROUPS HISTOGRAM

-- CANONICAL DISCRIMINANT FUNCTION 1 --



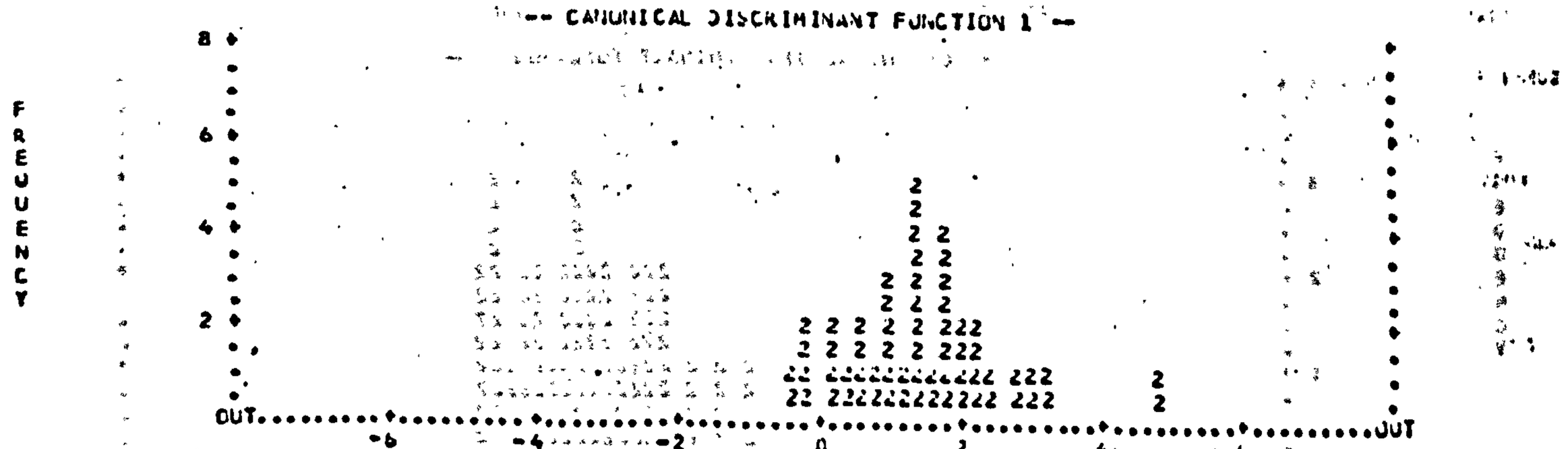
HISTOGRAM FOR GROUP 1 SUBFILE MEST

-- CANONICAL DISCRIMINANT FUNCTION 1 --



HISTOGRAM FOR GROUP 2 SUBFILE MAJR

-- CANONICAL DISCRIMINANT FUNCTION 1 --



CLASSIFICATION RESULTS -

ACTUAL GROUP	NO. OF CASES	PREDICTED GROUP MEMBERSHIP 1	2
GROUP 1 SUBFILE MEST	51	45 88.23	6 11.68
GROUP 2 SUBFILE MAJR	37	5 13.51	27 86.49

PERCENT OF GROUPED CASES CORRECTLY CLASSIFIED: 86.75%

SYMBOLS USED IN PLOTS

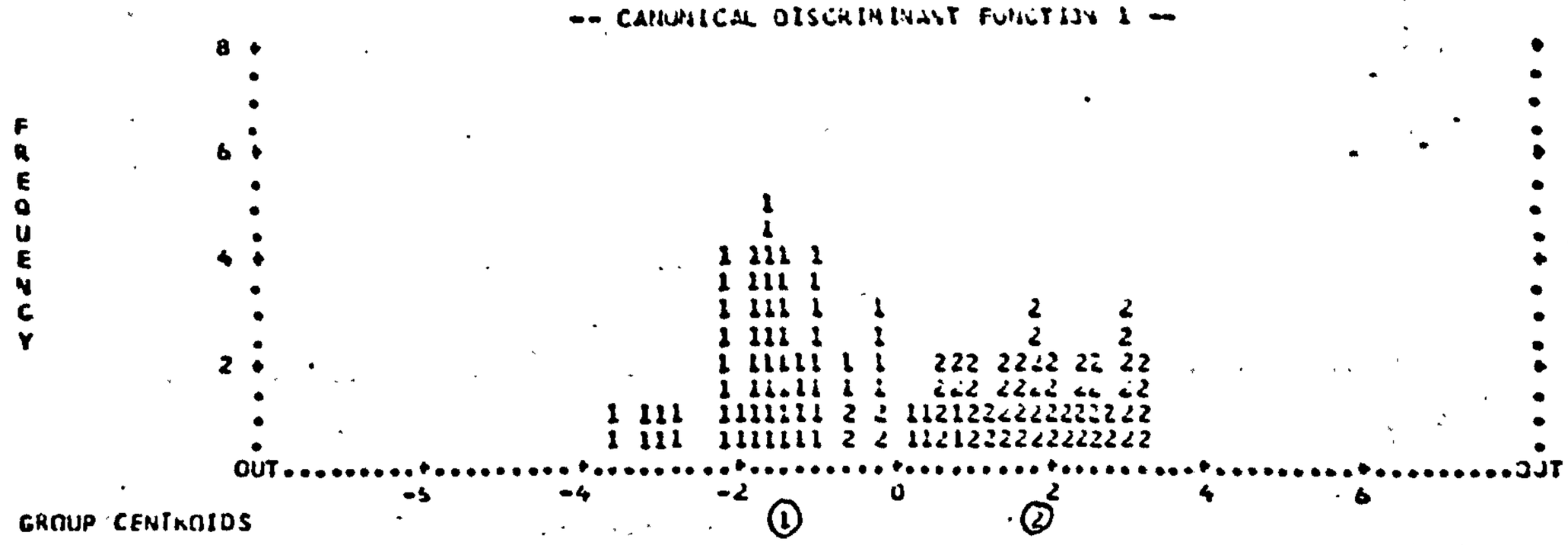
SYMBOL	GROUP	LABEL
1	1	SUBFILE FEST
2	2	SUBFILE FNJR

Group 1 – D. aurita ♀♀
Group 2 – D. marsupialis ♀♀

DISCRIMINANT ANALYSIS

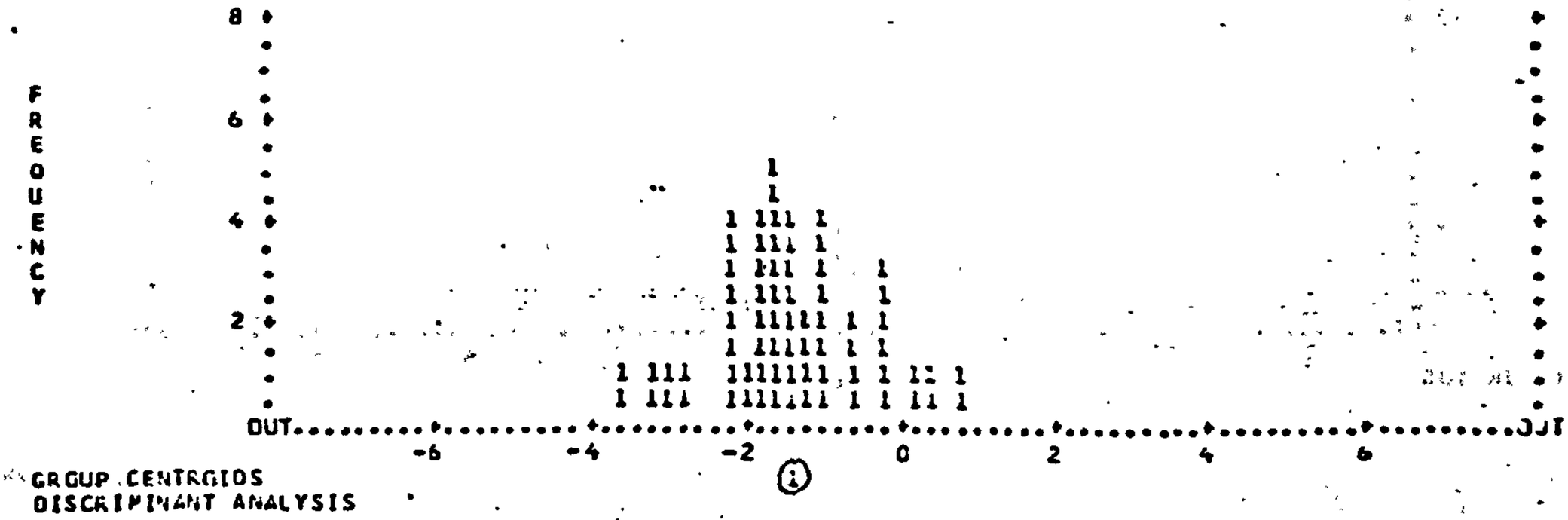
ALL-GROUPS HISTOGRAM

-- CANONICAL DISCRIMINANT FUNCTION 1 --



HISTOGRAM FOR GROUP 1 SUBFILE FEST

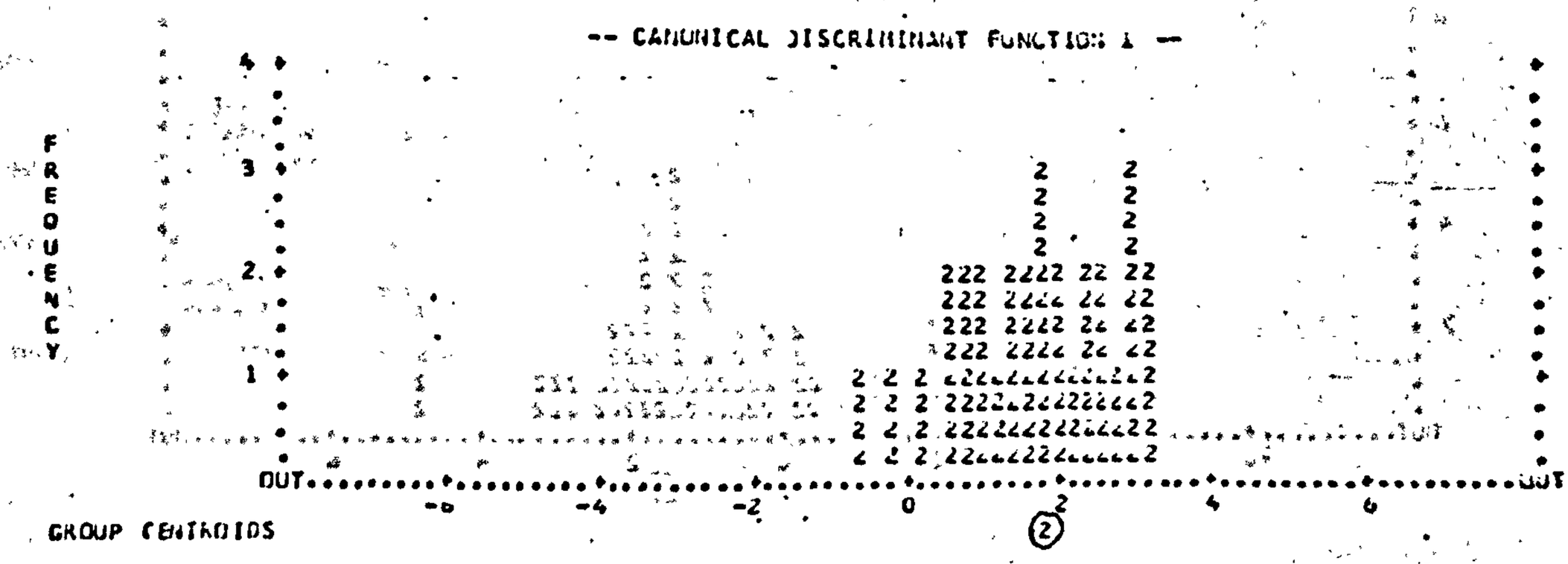
-- CANONICAL DISCRIMINANT FUNCTION 1 --



DISCRIMINANT ANALYSIS

HISTOGRAM FOR GROUP 2 SUBFILE FNJR

-- CANONICAL DISCRIMINANT FUNCTION 1 --



CLASSIFICATION RESULTS -

ACTUAL GROUP	NO. OF CASES	PREDICTED GROUP MEMBERSHIP 1	2
GROUP 1 SUBFILE FEST	30	23	3
		91.7%	8.3%
GROUP 2 SUBFILE FNJR	30	2	28
		6.7%	93.3%

PERCENT OF "GROUPED" CASES CORRECTLY CLASSIFIED: 92.92%